

A REVIEW OF THE PHYLOGENY AND CLASSIFICATION OF THE LEPIDOPTERA.

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(Ninety-six Text-figures.)

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INTRODUCTION.

It would be impossible for one who has not access to the necessary documents to give a history of the classification of the Lepidoptera. Fortunately a brief reference to three well-known works will give sufficient historical background to this essay.

The first is "A Manual of British Butterflies and Moths", in two volumes, the first published in 1857, the second in 1859, by H. T. Stainton. From this old work, which breathes a charm unknown to modern writings, I extract the following classification. To facilitate its understanding I have added a few words in parentheses.

Rhopalocera.	Geometrina.
Papilionidae (including Pieridae).	17 families.
Nymphalidae.	Pyrалidina.
Erycinidae.	17 families (including Hypenidae,
Lycaenidae.	noctuid genera <i>Earias</i> and
Hesperiidae.	<i>Halias</i> , Nolidae, and glyphi-
Heterocera.	pterygid genera <i>Choreutis</i> and
Sphingina.	<i>Simaethis</i>).
Zygaenidae.	Tortricina.
Sphingidae.	9 families.
Sesiidae (clear-winged Sphingidae).	Tineina.
Aegeriadae.	Exapatidae (Oecophoridae).
Bombycina.	Tineidae.
Hepialidae.	Micropterygidae.
Zeuzeridae.	Hyponomeutidae.
Notodontidae.	Plutellidae.
Liparidae (Lymantriadae).	Gelechidae.
Lithosiadae (Arctiadae).	Oecophoridae.
Chelonidae (Arctiadae).	Glyphipterygidae.
Bombycidae (Lasiocampidae).	Argyresthidae.
Saturnidae.	Gracilariidae.
Platypterygidae (Drepanidae).	Coleophoridae.
Psychidae.	Elachistidae.
Cochliopodidae (Limacodidae).	Lithocolletidae (Gracilariidae).
Noctuina.	Lyonetidae.
Trifidae.	Nepticulidae.
15 families (including the Cymato-	Pterophorina.
phoridae).	Pterophoridae.
Quadrifidae.	Alucitina.
9 families.	Alucitidae (Orneodidae).

Just as the lineaments and character of a future adult are already apparent in a young child, so we may see here the early stage of our modern classification. Looked at with scientific impartiality its excellencies outweigh its evident defects. Especially in the Tineina, for which Stainton was most directly responsible, while in other groups

he borrowed from other writers, we have a list of families closely corresponding to that given in the most recent work of Meyrick, who was himself primarily a microlepidopterist. The Rhopalocera and Bombycina call for little criticism. On the other hand, it must be admitted that Stainton's Sphingina consists of three widely unrelated families. His Noctuina are rightly separated into Trifidae and Quadrifidae,* but, like the Geometrina, Pyralidina and Tortricina divided into families, which are based on no structural characters, and I have not thought it necessary to transcribe their names.

In 1895, just thirty-six years later, a great advance in our knowledge was made by the appearance of "A Handbook of British Lepidoptera" by Edward Meyrick with the following classification.

Caradrinina.	Pyralidina.
Arctiadae.	Phycitidae.
Caradrinidae (Noctuidae).	Galleriadae.
Plusiadae (Noctuidae).	Crambidae.
Oceriadae (Lymantriadae).	Pyraustidae.
	Pyralidae.
Notodontina.	Pterophoridae.
Hydriomenidae (Larentiadae).	Orneodidae.
Sterrhidae.	
Geometridae.	Psychina.
Monocteniadae (Oenochromidae).	Psychidae.
Selidosemidae (Boarmiadae).	Zeuzeridae (Cossidae).
Polyplocidae (Cymatophoridae).	Zygaenidae.
Sphingidae.	Heterogeneidae (Limaecodidae).
Notodontidae.	
Saturniadae.	Tortricina.
	Epiblemidae (Eucosmidae).
Lasiocampina.	Tortricidae.
Drepanidae.	Phaloniadae.
Endromidae.	Trypanidae (Cossidae).
Lasiocampidae.	
	Tineina.
Papilionina.	Aegeriadae.
Nymphalidae.	Gelechiadae.
Satyridae.	Oecophoridae.
Erycinidae.	Elachistidae.
Lycaenidae.	Plutellidae.
Pieridae.	Tineidae.
Papilionidae.	
Hesperiadae.	Micropterygina.
	Hepialidae.
	Micropterygidae.

Here we have a classification based on defined structural characters. While characters derived from the structure of the tongue, palpi, antennae (especially in the male), legs (especially the posterior pair), wing-coupling apparatus, and the presence of scale-tufts on the forewings are not neglected, the definitions depend chiefly on the neurulation, which has been studied with much care. Except in the Tineina, the families have been firmly established, if we omit the inclusion of the Nolidae and some noctuid genera in the Arctiadae, and the unnecessary division of the Noctuidae into two families. The superfamilies do not rest on such a secure basis. The Notodontina, Lasiocampina and Psychina are open to criticism as heterogeneous groups. The inclusion of the Cossidae in the Tortricina has already been abandoned (in 1927), and in my opinion the separation of the Tortricina from the Tineina is not justified.

* These words are good Latin, just as trifid and quadrifid are good English, and have no connection with Greek names ending in -idae or -inae. It is an error to transliterate them into Trifinae and Quadrifinae, as has been done by some.

A noteworthy characteristic of Meyrick's work was that he never accepted his own classification as final, and in "A Revised Handbook of British Lepidoptera" published in 1927 he introduced several changes.

Caradrinina.

Arctiadae.
 Nolidae.
 Hylophilidae (several noctuid genera).
 Caradrinidae.
 Plusiadae.
 Oceriadae.

Notodontina.

Sterrhidae.
 Geometridae.
 Hydrimenidae.
 Monocteniidae.
 Selidosemidae.
 Polyplocidae.
 Sphingidae.
 Notodontidae.
 Saturniadae.

Papilionina.

Papilionidae.
 Nymphalidae.
 Satyridae.
 Erycinidae.
 Lycaenidae.
 Pieridae.

Hesperiana.

Hesperiidae.

Drepanina.

Drepanidae.

Pyrilidina.

Phycitidae.
 Galleriadae.
 Crambidae.
 Pyraustidae.
 Pyralidae.
 Pterophoridae.

Lasiocampina.

Endromidae.
 Lasiocampidae.

Psychina.

Heterogeneidae.
 Zygaenidae.
 Psychidae.
 Zeuzeridae.

Tortricina.

Phaloniadae. Tortricidae.
 Eucosmidae.

Tineina.

Group 1. Gelechiidae.	Blastobasidae.
	Cosmopterygidae. Oecophoridae.
2. Orneodidae.	
3. Aegeriadae.	Heliodinidae.
	Glyphipterygidae.
4. Elachistidae.	Scythridae.
	Hyponomeutidae.
5. Coleophoridae.	Epermeniidae.
	Plutellidae.
6. Lyonetiadae.	Lamproniadae.
	Adelidae.

Nepticulina.

Nepticulidae.

Micropterygina.

Hepialidae.
 Micropterygidae.

CRITICISMS OF MEYRICK'S CLASSIFICATION.

We owe a great debt to Meyrick's work. Whatever future changes may be made, and no classification can remain static, while our knowledge continues to increase, we are indebted to him for a classification based on structure. For this he is entitled to our respect. It should be our purpose to build on the foundation he has laid, keeping an open mind on matters that may appear doubtful, and endeavouring to be guided only by facts, knowing well that any classification that we may propose will itself be changed by those who may come after us. In this spirit I propose to offer the following criticisms.

(1). In his revised classification, the family Arctiadae has been purged of extraneous elements, and the family Nolidae has been recognized as a distinct family. His conception of the family Hylophilidae is unfortunate, being based on a single character, the long anastomosis of 8 of the hindwings with the cell, a character which occurs in wholly unrelated families such as the Larentiidae, Oenochromidae, Boarmiidae, Drepanidae, and in the genus *Stilbia* recognized by himself as a noctuid. These are instances of "parallel evolution", which is of common occurrence in the Lepidoptera. The genera

of his "Hylophilidae" are close allies of other noctuid genera, in which this anastomosis is short and sub-basal.

(2). The Noctuidae is a very homogeneous family and its division into two families on a character which is not always distinctive is not justified.

(3). The superfamilies Notodontina and Psychina contain families not closely related. This and the following criticisms are more fundamental and will be discussed at some length.

(4). The position of the Papilionina and their severance from the Hesperiana require closer examination.

(5). The separation of the Tortricina from the Tineina is not justified.

(6). The morphological differences between the Hepialidae and the Micropterygidae are too great to allow their inclusion in a single superfamily.

(7). The classification lacks major divisions.

THE MORPHOLOGY OF THE WINGS OF LEPIDOPTERA.

Although Meyrick's classification depends mainly on the neururation, he makes no use of some of its most important features. This is well shown by Figure 1 copied from his Revised Handbook. His assumed type of neururation shows in the forewing three anal veins, 1a, 1b and 1c (which is Cu2), a central cell from which arise veins 2 to 11, and a subcostal vein 12. The hindwing differs in having only six veins arising from the central cell. He mentions the occasional occurrence in some earlier forms of a forked "parting-vein" traversing the cell of both wings and another "parting-vein" cutting off the upper posterior area of the cell in the forewing. So far good: but these complications are denied any importance in the classification of the Lepidoptera, though he admits that they may have some bearing, when considering its relationship to other orders.

In my opinion the variations in the peripheral veins, which Meyrick has studied so carefully, give good generic characters, but are of minor importance in showing the affinities of families and superfamilies, which are often better indicated by the basal vein trunks. His assumed type of neururation, in spite of its apparent simplicity, is not primitive, but has resulted from very remarkable changes affecting the really primitive form. The whole course of evolution in the lepidopterous wing has been from complexity towards simplicity by loss or coalescence of veins. It has been an evolution by asthenogenesis, and has often followed parallel lines in groups not nearly akin. Confining ourselves for the moment to the Lepidoptera Heteroneura, I present Figure 2 as the primitive neururation. While not the exact neururation of any existing genus, it combines the most primitive characters of several genera of Cossidae. Here the forewing has four main trunk veins, the subcostal, the radial with five branches, the median with three, and the cubital with three, together with two concurrent anal veins. In the hindwing there are three anal veins but only two radial, the radial sector being unbranched and the first radial running into the subcostal. All these longitudinal veins are formed around the tracheae of the pupal wings. In addition, there are three cross-veins which arise independently of the tracheae. This will be made clearer by the accompanying diagram (Fig. 3). The radius divides at the first radial fork into the first radial and the radial sector; the latter divides at the second radial fork, and these branches again divide into the second and third radial and the fourth and fifth radial respectively. The discoidal cell or areole is completed by an inter-radial cross-vein. Within the main cell the median divides into two branches, each of which again divides into two, the fourth branch joining with the uppermost cubital branch to form a compound vein. The median cell is closed by the intermedian cross-vein, and the main cell, in which it is enclosed, is completed by the radio-median cross-vein. The inter-radial cross-vein tends to disappear in many groups, being replaced by anastomosis between R3 and R4. This completes the areole.

By its conciseness and freedom from ambiguity the numerical notation adopted by Meyrick is well adapted for the description of generic and specific differences, but is defective when applied to the definitions of higher groups. In this review I have accordingly adopted the notation proposed by Comstock and Needham as modified by Tillyard. The following scheme illustrates the relationship of these two notations.

Forewing.				Hindwing.			
Vein 12	Subcostal	Vein 8	Subcostal
" 11	First Radial	(Wanting)	First Radial
" 10	Second "	" 7	Radial Sector
" 9	Third "	" 6	First Median
" 8	Fourth "	" 5	Second "
" 7	Fifth "	" 4	Third "
" 6	First Median	" 3	Cubital 1a
" 5	Second "	" 2	" 1b
" 4	Third "	" 1a..	" 2
" 3	Cubital 1a	" 1b..	Conjoint first and second Anals
" 2	" 1b	" 1c..	Third Anal
" 1a..	" 2				
" 1b..	First Anal				
" 1c..	Second "				

THE HOMONEURA.

The Lepidoptera fall into two natural divisions or suborders the Homoneura (or Jugata) and the Heteroneura (or Frenata). In the former the radial sector divides into four (rarely three) veins in both fore- and hindwings; and wing-coupling is effected by a process at the base of the dorsum of the forewing known as the jugum. The suborder is divisible into two superfamilies, the Micropterygoidea and the Hepialidoidea, the former being the more primitive, and composed of three families. Although these are subfamilies in Meyrick's classification (Meyrick, 1912), the differences between them are sufficient to justify family rank. The most primitive family is the Micropterygidae. Its neururation, shown in Figure 4, is in most respects similar to that of the most primitive family, the Rhyacophilidae, of the Trichoptera, though with a few not unimportant differences. Both neururations show striking resemblance to that of *Belmontia*, a fossil wing from the Upper Permian. For this, Tillyard has created the order Paramecoptera, which he believes to be the common ancestor of the Trichoptera and Lepidoptera (Tillyard, 1919).

The family Micropterygidae is primitive not only in neururation; but they are the only Lepidoptera that possess functional toothed mandibles and maxillae with primitive short galea and lacinia as well as with long five-jointed palpi (Philpott, 1927). The Eriocranidae have lost the mandibles in the imago, and the maxillae are specialized by the loss of the lacinia and the transformation of the galea into a short haustellum, although the palpi are similar. In the forewing the inter-radial cross-vein is not developed and consequently there is no areole. The larvae of the two families differ greatly. In the Mnesarchaeidae the mandibles are absent, the maxillae have a well-formed haustellum with very small three-jointed palpi. The radial sector is three-branched in both wings and there is no areole. It should be noted that in Figure 4 the hindwing differs from the forewing in several points. The first radial runs into the second subcostal and its basal portion is obsolete; the second cubital is scarcely developed; and the anal veins have been much reduced.

The neururation of the Hepialidae is remarkably constant (Philpott, 1926). With the exception of the presence of a weak branch of the subcostal of the forewing in *Sthenopsis*, which I can confirm from my own observation, and the degraded neururation of the hindwing in *Elthamma* (*Perissectis*), which is present only in the male, and therefore of little significance, there seem to be no noteworthy variations. In Figure 5 both wings are alike except in the anal area. The median fork is always near the base, and an intermedian cross-vein closes the median cell, but there is no areole. In the Micropterygoidea the median fork is more distal, and intermedian cross-vein and median cell are absent. In the Hepialidae the first radial is always simple, and the junction of the fourth median with the uppermost branch of the cubital is strongly angled.

Recently in Australia and South Africa genera have been discovered which are rather closely allied to the Hepialidae, but have been considered to represent new

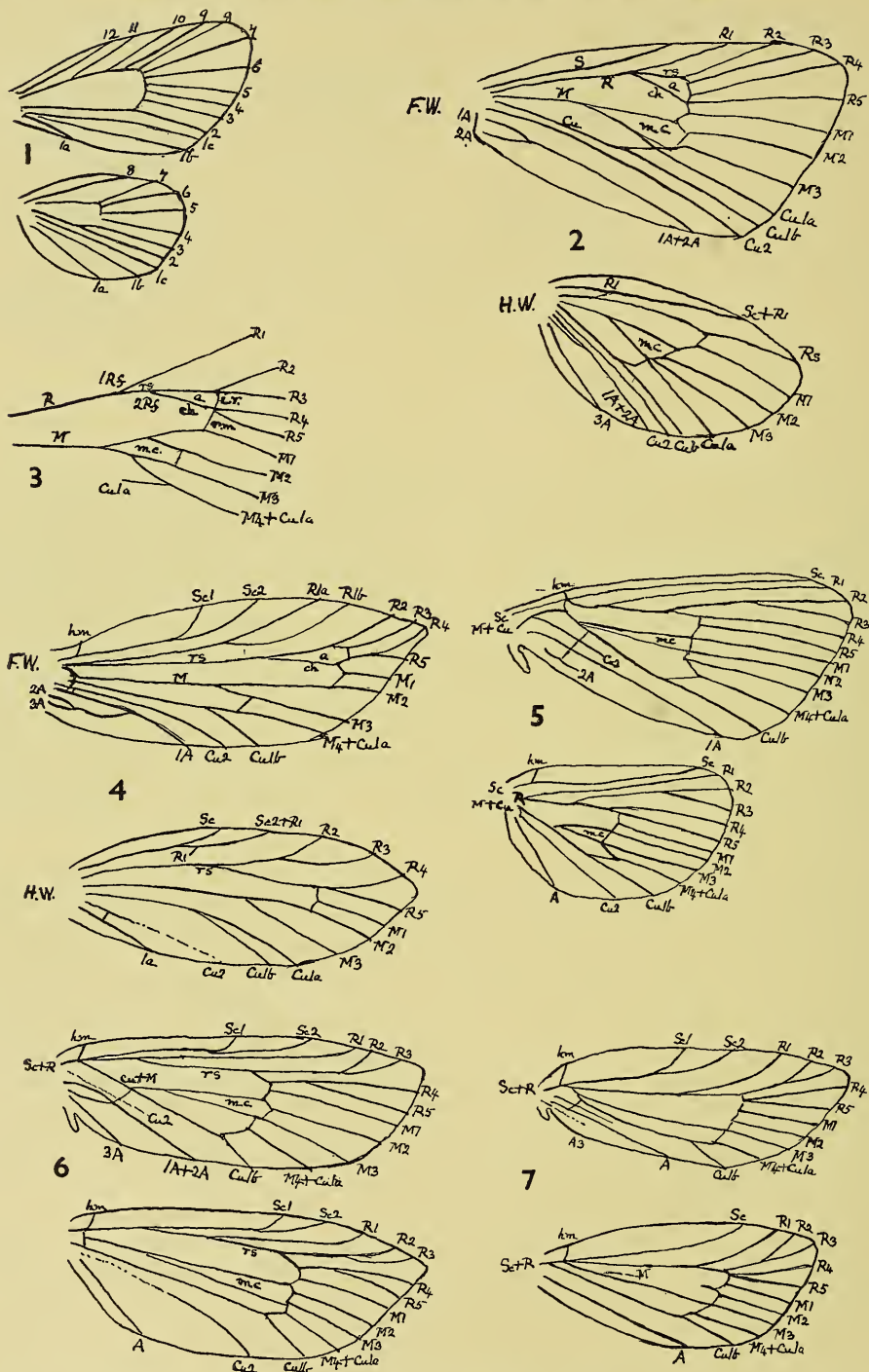


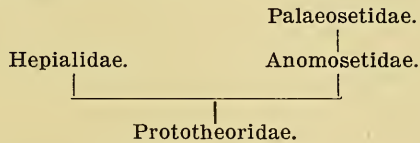
Fig. 1.—Meyrick's assumed type of neuration. Fig. 2.—Diagram of protocossid neuration. Fig. 3.—Diagram of radial and median veins. Fig. 4.—*Sabatinca incongrualis* Wlk. (after Philpott). Fig. 5.—*Trictena argentata* H-Sch. Fig. 6.—*Prototheora* sp. (after Philpott). Fig. 7.—*Anomoses hylecoetes* Turn.

Sc., Subcostal; R., Radial; M., Median; Cu., Cubital; A., Anal; a., Areole; m.c., Median cell, i.r.f., First radial fork; 2.r.f., Second radial fork; r.s., Radial sector; i.r., Inter-radial; r.m., Radio-median; i.m., Intermedian.

families (Turner, 1918; Philpott, 1928). Their neuration is shown in Figures 6, 7 and 8. Their differences from Hepialidae and each other may be tabulated as follows:

<i>Hepialidae.</i>	<i>Prototheoridae.</i>	<i>Anomosetidae.</i>	<i>Palaeosetidae.</i>
Subcostal rarely forked in f.w., never in h.w.	Subcostal forked in both wings.	Subcostal forked in f.w. only.	Subcostal forked in f.w. only.
Median vein forked.	Median vein forked.	Upper branch of median absent.	Upper and lower branches of median absent.
M4 strongly angled with Cula.	M4 slightly angled with Cula.	M4 slightly angled with Cula.	M4 absent.
F.w. with one or two anal veins, 1A and 2A sometimes looped.	F.w. with three anal veins, 1A and 2A looped.	F.w. with two anal veins not looped.	F.w. with one anal vein.
Maxillae and palpi rudimentary.	Maxillae with small haustellum and rudimentary palpi.	Maxillae with small haustellum and short palpi.	Maxillae absent.
Tibial spurs absent.	Tibial spurs present.	Tibial spurs present.	Tibial spurs absent.

In my opinion we must either include all these groups in the Hepialidae, or recognize four families, of which the Prototheoridae and Anomosetidae are the most nearly akin. When we consider the amount of difference that separates many families in the Heteroneura, I think we should not hesitate to adopt the latter alternative. This has the advantage of making clearer the mutual relationship of the groups involved, which may be represented as follows:



THE HETERONEURA.

SOME NEURATIONAL CHARACTERS OF FUNDAMENTAL IMPORTANCE.

The classification of the Heteroneura is a much more difficult problem, and cannot be approached without a preliminary discussion of some points in their structure, which have not, I think, as yet received sufficient consideration.

In this classification all structural characters should be carefully considered, not excluding those of the larval and pupal stages, but we have to depend principally on differences in the neuration of the wings. On account of the tendency to the loss of veins in almost all the families, and of course also in the superfamilies, we must always be on our guard against the fallacies of parallel evolution and asthenogenesis. Against this we have two safeguards. Most of the families are natural groups well defined by a combination of characters and having their extreme forms more or less connected by intermediate genera. In them we may observe the process of simplification by asthenogenesis, the intermediate steps of which are fortunately preserved in existing genera. We are therefore justified, when endeavouring to understand the mutual relationships of these families, in ignoring their more specialized genera. In other words, the relationships of families are the same as those of their more primitive genera. Unfortunately some families lack the primitive genera, which we may fairly assume once existed. We have no fossilized wings in this order, as in many other orders of insects, by which to test our assumptions. But we are not left wholly without resource. In the Lepidoptera (unlike the Trichoptera) the wing nervures (except the cross-veins) are developed in the pupal wings along the lines of the tracheae. We may therefore obtain great assistance from studies of the pupal tracheation and its gradual development into the structure of the imaginal wings. This line of research was originated by Comstock and Needham (1898-1899), and has been ably followed by Comstock (1918) and Tillyard (1919). Already it has given us help in difficult cases, and very much more help may be

confidently expected from it in the future. Unfortunately the study of the pupal wings of Lepidoptera has been much neglected. A profitable field of research lies before those who will master its technique and will have the patience to apply it in the study of cases in which the study of the adult wings leaves us at present in some uncertainty.

The importance of these preliminary remarks will become more evident as we proceed to examine the value of some neuration characters, which have been too much neglected in the classification of the Lepidoptera. I refer especially to the variations in the main trunks of the median and radial veins. A combination of the most primitive characters in the Cossidae is here illustrated (Figs. 2 and 3). In that family the median vein always persists, and there is almost always a strong vein within the cell running from the radial sector to the outer edge of the cell. This is the common stalk of the fourth and fifth radial veins, which, for reasons which will appear presently, I have called the *chorda* (Turner, 1918). In some of the genera of the Cossidae there is a tendency towards narrowing of the median cell in both wings, as in *Holocerus*, which may proceed so far as to cause its disappearance, as in *Stygia*, the primary branches having coalesced. Occasionally in the latter genus a small median cell may persist in the forewings. In the great bulk of the Heteroneura, however, these veins are totally absent, in others they are much reduced or vestigial. Yet they are always present, usually accompanied by the chorda, in the pupal wing, as was first discovered in the Rhopalocera (Comstock and Needham, 1898).

We will now pass to the Tineoidea, whose neuration is more primitive than that of many families, though less so than that of the Cossidae. Here all trace of the median trunk and the chorda are commonly absent, as in Figure 11. It will be noticed that here we have the neuration assumed to be primitive by Meyrick (Fig. 1). Actually this is a secondary condition due to asthenogenesis. That this is so is proved by the existence of these veins in a more or less attenuated condition in more than a few genera such as *Isotrias* (Fig. 12) and *Cerostoma* (Fig. 13) (Turner, 1918). Finally, it has been found that they are present in the pupal wings of several genera (Tillyard, 1919) and undergo the same changes during the maturation of the wing as occur in the Rhopalocera. This obliteration of the basal median tracheal trunks affects the origin of the peripheral veins. M1 becomes approximated to R5, M3 to Cula, M2 is also frequently approximated towards the cubital, as in the Noctuoidea (Fig. 68), but it may retain its original position or become approximated to the radial as in the Geometroidea (Fig. 53); these changes resulting from these veins being captured by tracheae from the cubital or radial trunks (Tillyard, 1919). Similarly, in the hindwing, M2 may be attracted to the cubital as in the Noctuidae Quarifidae (Fig. 68) or remain in its original position, becoming obsolete through tracheal deprivation as in the Noctuidae Trifidae (Fig. 69); less often it is attracted to the radial in several families. These variations in the origin of M2, especially in the forewings, have been found of great service in classification.

The primitive areole in the forewings is persistent in some families, absent in others, and present in the more primitive genera of many. The methods of its disappearance vary. It is important to recognize that this disappearance may result from three different causes: (1) By obsolescence and loss of the chorda, the name which I have given to the lower limb of the radial fork, that is, the trunk of R4 and R5, which lies within the cell. I have already shown that this occurs in the Tineoidea. The lepidopterous cell after this obsolescence has been completed consists of both cell and areole, and I have called it an areocel (Fig. 14) (Turner, 1918). (2) By gradual approximation and eventual fusion of the chorda with the trunk of R2 and R3, which I have illustrated in the Cossidae (Fig. 15) (Turner, 1918). This process occurs in many groups. (3) The anastomosis of R2 with R3, that replaces the inter-radial cross-vein in the higher groups may be broken by dissociation, as occurs frequently in the Cymatophoridae, Oenochromidae, and the Sarrhothripinae subfamily of the Noctuidae, usually as an individual variation within the species.

THE PRIMARY DIVISIONS OF THE HETERONEURA.

Asthenochorda and Sthenochorda.

The classification which I propose is based primarily on the remarkable changes in the pupal wing discovered by Comstock and Needham (1898-9) in the Rhopalocera,

and by Tillyard (1919) in the Tineoidea, supported by my own observations on the imaginal wings of the latter group (1918). These concern (1) the loss of the median vein and its two primary branches, accompanied (2) by a similar obsolescence or disappearance of the chorda, which results in the merging of the primitive areole with the primitive lepidopterous cell to form what I have called an areocel (1918). All the superfamilies in which this occurs I have grouped into a Primary Division, to which I have given the name *Asthenochorda*. In this division the chorda has completely disappeared in the imaginal wing (though represented in the pupal neuration) in all except the Tineoidea. There it sometimes persists in a weak or vestigial condition, or very rarely as a fairly strong vein. This division includes the Rhopalocera, Zygaenoidea, Pyraloidea, Pterophoroidea and Tineoidea. Perhaps the inclusion of the Rhopalocera with these four superfamilies will come as a shock to some of my readers. But a little study should convince them that this proposal is not so revolutionary as may appear at first sight (Figs. 17 and 18). It is now many years since Meyrick (1895, p. 326) declared that the nearest allies of the Hesperidae are the Thyrididae. Long before this, the older conception that the Hesperidae were closely allied to the Castniidae was shown to be baseless by Westwood (1876, p. 157), who referred particularly to the primitive genera *Megathymus* (ibid., p. 205) and *Euschemon* (Pl. 29, f. 26).

The Rhopalocera, however, show some characters not found elsewhere in the *Asthenochorda*. They are:

(1). The presence of a humeral veinlet (or precostal spur) at the base of the hindwing. This appears to be always present except in the Lycaenidae and some genera of the Pieridae, which, presumably, have lost it.

(2). The loss of Cu₂ of the hindwing. In the Tineoidea this has been lost sometimes by asthenogenesis, but it is present in all the primitive genera of that group.

(3). The presence of R₁ in the hindwings of the Papilionidae and Elymnianae, running into the subcostal and so forming a precostal cell (Fig. 21).

(4). The presence of a cubito-anal cross-vein in the forewing in the Papilionidae (Fig. 20).

(5). The presence in the forewing of the Papilionidae of a second anal vein running into the dorsal margin (Fig. 20).

Of these, (2) and (3) are not uncommon in the *Sthenochorda*. A few of the *Sthenochorda* have precostal pseudoneuria but these appear to be recent adaptations, present or absent in closely allied genera, and not in my opinion homologous with the precostal spur of the Rhopalocera, among whom it appears to be a fundamental character. Character (4) is a unique development in the Heteroneura, but a similar cross-vein occurs in the Hepialidae. Whether this character has been directly derived from a common ancestor or has developed independently in the Papilionidae is doubtful. Character (5) is also unique in the Heteroneura, though an incomplete prolongation of A₂ beyond A₁ has been noted in a few genera.

In consequence of these differences, I propose to divide the *Asthenochorda* into two Subdivisions, the *Rhopalocera* and the *Microptila*.

For all the remaining Heteroneura I propose the name *Sthenochorda*. In them the chorda is always strong, but frequently fused with the radial sector and the common stalk of R₂ and R₃, so that the areole disappears by coalescence. When this has happened, R₃ and R₄ are usually stalked. The "tortriciform neuration", characteristic of the most primitive genera of the Microptila, is never seen in this subdivision. There is no difficulty in following the steps by which the areole has disappeared in some genera of the Cossoidea and of the Drepanidae, Notodontidae, Geometroidea and Noctuoidea. To the *Sthenochorda* I refer also the Sphingoidea, Uranoidea, Bombycoidea, Lasiocampoidea and Psychoidea. In these the areole is never present in the adult wing, and R₃ is always stalked with R₄ (Fig. 16). Probably the areole may sometimes be found represented in the pupal wing, but Tillyard has shown that in *Doratifera* of the Psychoidea it has been eliminated by transference of R₃ to R₄ in the pupa, and so also in *Antheraea* of the Bombycoidea. In how many forms this has occurred we do not yet know.

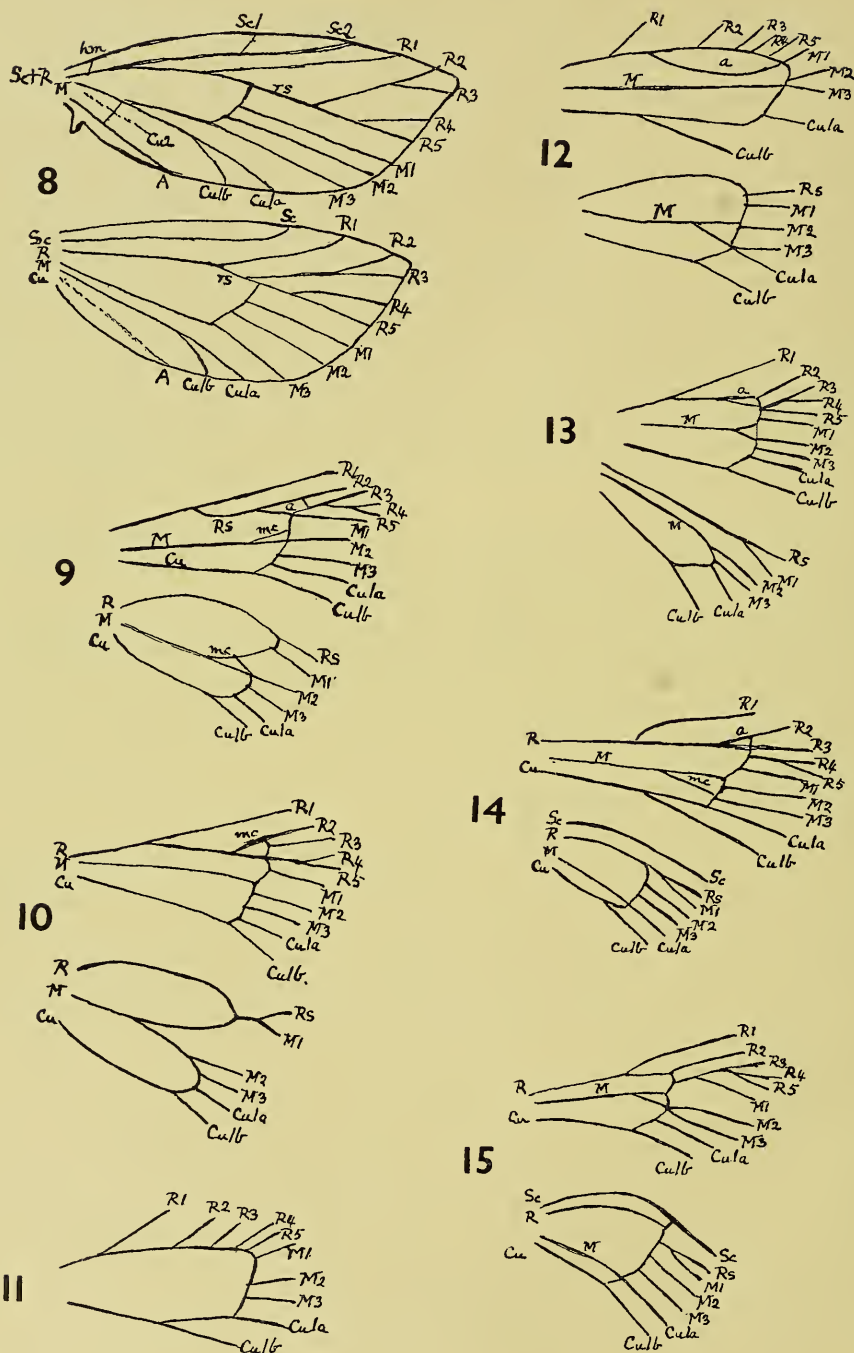
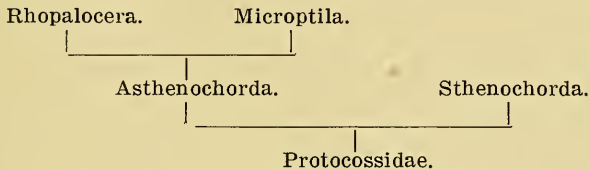


Fig. 8.—*Palaeoses scholastica* Turn. Figs. 9-15.—Diagrams of radial and median veins. Fig. 9.—*Holocerus nobilis* Stand. Fig. 10.—*Stygia australis* Latr. Fig. 11.—*Tortrix viridana* Lin. Fig. 12.—*Isotrias hybridana* Hb. Fig. 13.—*Cerostoma radiatella* Don. Fig. 14.—*Lentagena tristani* Schaus. Fig. 15.—*Acyttara tigrata* Schaus.

Loss of the areole by dissociation occurs occasionally in the Sthenochorda, but never in the Asthenochorda. This loss, which occurs mostly when the areole is very long and narrow, is caused by the failure of the basal part of R3, which anastomoses with R4, to chitinize. In consequence R2 is stalked with R3, and R4 with R5, as in *Castulo* (Arctiadae) (Fig. 19).

It happens that, with the exception of the Zygaenoidea, whose affinities have not hitherto been rightly understood, the Microptila have long been known as an undefined group under the name of Microlepidoptera or "micros". Although this name has originated from the small size of the great majority of its species, size has never been regarded as its essential character. This has been so even in Europe, but in Australia it is still more evident. In this region many species of Geometroidea, Arctiadae, Nolidae and Noctuidae are much smaller than many species of the Xyloryctidae, Oecophoridae, Hyponomeutidae, Tineidae and other families of the Microptila.

The major divisions of the Heteroneura may be represented by the following diagram.



The Protocossidae is a hypothetical family conceived as combining the primitive cossid neururation (Fig. 2) with the five-jointed maxillary palpi of the Tineidae. Like the Hepialidae, members of this family were probably stem or root feeders and developed before the advent of flowering plants. They cannot, however, have developed from the Hepialidae, which is the termination of an early offshoot of the lepidopterous stem with rigid neurational characters. Their connection with the stem from which arose the Hepialoidea and Micropterygoidea, though real, must have been very remote.

SOME OBSERVATIONS ON NEURATION.

I propose to record here a few further observations, which are of importance in the classification of the Lepidoptera.

(1). *The Anal Veins of the Forewing.*

Originally there were three anal veins, but the third anal is preserved only in a few of the Homoneura. In *Sabatinca* alone of the Micropterygoidea it is present, the three anals forming a double loop (Fig. 4). In the Hepialidae it appears to be always absent, but in *Prototheora* it is present as a distinct vein running independently to the wing-margin (Fig. 6). A similar but weaker vein can be traced in *Anomoses* (Fig. 7). In the forewings of the Heteroneura there are never more than two, which arise from the base of the wing and unite to form a U-loop (3A having disappeared), as is shown in the accompanying figures, which illustrate also the steps by which it becomes replaced by a single vein. In the Pyraustidae the loop, when present, has a characteristic boat-shape (Fig. 33). Simplification in the majority of cases is accomplished by the obsolescence of the lower limb (A2) of the loop (Fig. 24). Only in one genus, *Endrosis*, have I so far observed obsolescence of the upper limb (1A); and in none have I seen a coalescence of the two limbs. In *Synemon*, in *Cerura*, and in two genera of Noctuidae (Figs. 26 and 51), I have observed a prolongation of 2A beyond the loop comparable to that in the Papilionidae, though less marked (Fig. 25).

(2). *The Anal Veins of the Hindwing.*

Three anal veins are present in the more primitive Homoneura and Heteroneura (Fig. 25). Tillyard has shown (1919) that in the pupal tracheation of the most primitive genera of both groups 1A runs very close to, or actually fuses with, Cu2 near its base, then separates and approaches 2A. In the imaginal wing scarcely a trace of this course remains. 1A and 2A fuse, leaving a small V-loop at their base. By reduction this loop tends to disappear in many cases as does 3A.

(3). *The First Radial and Subcostal of the Hindwing.*

What is commonly called the subcostal in the Heteroneura is really a compound vein Sc + R1 (Fig. 21b). In the more primitive genera of many families R1 runs into Sc to form this compound vein. In others R1 disappears, being completely fused with Sc from near the base of the wing (Figs. 28 and 67). An important aid is given to phylogeny and classification by these changes.

(4). *The Second Cubital Vein.*

This is normally a weak vein in both wings, and it shows a strong tendency to become obsolescent or absent. In the Hepialoidea (Fig. 5) it is normally developed in the hindwing, but is weakly developed from the base in the forewing, and disappears altogether before half its normal course is run. In the Rhopalocera it is always absent in both wings (Fig. 20). In the Tineoidea it is absent or vestigial in the forewing, only its terminal end being, in some, developed for a short distance (Fig. 36); but is normally or weakly developed in the hindwing. In the Pyraloidea (Fig. 33) it is absent, or rarely vestigial, in the forewing; in the hindwing it is normally developed or weak. In the Pterophoroidea (Figs. 34 and 35), on the contrary, it is normally developed in both wings, as also in the Zygaenoidea (Figs. 29 and 30).

In the taxonomy of the Sthenochorda the variations in Cu2 are important. In the Cossioidea it is normally developed in both wings in the Cossidae (Fig. 2) but in the hindwing only in the Arbelidae and Argyrotylidae. In the Castnioidea it may be developed in the forewing only (Figs. 92-94). In the Psychoidea it is present in both wings (Figs. 89 and 90). In the more primitive genera of the Tineoidea its apical portion only is developed in the forewing, but the whole vein in the hindwing.

(5). *The Second Median Vein.*

I have heard the objection raised, that neurulation is an unsatisfactory guide to classification, because it is so often variable. The fact alleged is correct; the deduction is fallacious. It reflects an *a priori* attitude and a want of observation. Some details of neurulation, for instance, the approximation, stalking, or even the coalescence of certain veins, may occur within the limits of a species; that of others may give good generic characters, others again are characteristic of whole families or even superfamilies. Only by careful study can we learn their relative importance. There is another *a priori* assumption that has proved misleading to some. This is the supposition that a character that has proved valuable in one group will necessarily prove of equal value in another group. Nature has no respect for this assumption. For instance, the stalking or coalescence of R4 and R5 of the forewing is a family character in the Oecophoridae, but is not always of generic value in the Hyponomeutidae and Glyphipterygidae. Again, the coalescence of these veins is a useful generic character in the Oecophoridae, but in rare instances occurs as an individual abnormality in a genus, in which these veins are normally stalked. It would be possible, but is not necessary, to give other similar instances.

Experience has shown that variations in the origin of M2 of the forewings are of much higher value than changes in other peripheral veins. For this we can see a reason. These variations arise from the loss in the pupal wing of the tracheae, on which are formed the median veins within the cell. As a consequence M2 in the pupal wing may be captured by a tracheal branch arising from Cu1a, with the result that in the imaginal wing M2 becomes approximated in origin to M3 (Tillyard, 1919). This does not always occur; M2 may retain its original position, or may become approximated to M1; for M1 is captured by a tracheal branch from R5, and this sometimes captures M2 also.

In the hindwing M2 may remain in its original position either fully developed or, as a result of diminished tracheal supply, weakly developed or obsolescent or completely absent. On the other hand, owing to capture of its trachea by the cubital, its origin may be more or less approximated to M3, in which case the vein remains fully developed. This is well illustrated in the Noctuidae by the differences between the hindwings of the Trifidae and the Quadrifidae (Fig. 69). Much less commonly M2 moves in the opposite

direction, its origin becoming approximated to that of M1. These differences are valuable as characters for the definition of genera, and sometimes of subfamilies or families, but carry less weight than the corresponding variations in M2 of the forewing.

In the Rhopalocera, M2 is inconstant in position; it does not, as in the other two divisions of the Heteroneura, give us any guide in the discrimination of families. In the Hesperidae the subfamily Pamphilinae has this vein approximated to M3, whereas in the other subfamilies it arises midway between M1 and M3 (Fig. 28).

In the Microptila, the Zygaenoidea have M2 always approximated to M3 in the forewing, but only occasionally in the hindwing (Fig. 29). The Pyralioidea have M2 approximated to M3 in both wings, except in the Tineodidae and the genus *Addaea* (Thyrididae). In the forewing these veins may be stalked or coincident. In the Pterophoroidea the primitive genus *Agdistis* shows the same approximation in the forewing, but in the hindwing these veins are coincident (Fig. 34). In the cleft-winged genera the relations of these veins are obscured (Fig. 35). In the Tineoidea, after excluding those that have undergone extreme reduction of veins, M2 is usually approximated to M3 in both wings, but there are many exceptions, in which it arises from the midway position in one or both wings.

In the Sthenochorda the variations in M2 of the forewing are of much value in distinguishing superfamilies. It is approximated to M3 in the Cossoidea, Castnioidea, Psychoidea, Lasiocampoidea, Drepanoidea and Noctuoidea. This approximation is always distinct but varies in degree. For instance, in the Cossidae the most primitive genera have these veins moderately but not closely approximated, but in most of this family the approximation is more pronounced, and rarely may result in these veins becoming connate. In the higher groups the approximation is sometimes replaced by stalking or coalescence.

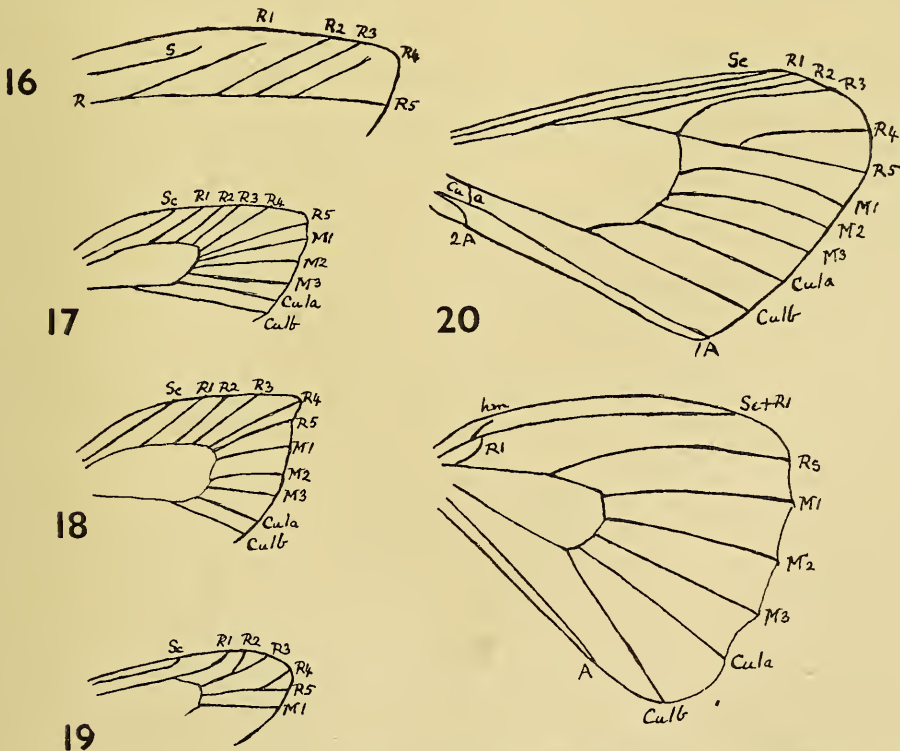


Fig. 16.—*Doratifera vulnerans* Lewin. Part of pupal forewing showing transference of R3 to stalk of R4 and R5 (Tillyard). Fig. 17.—*Hesperia tages* Lin. Fig. 18.—*Strigina scitaria* Wlk. Fig. 19.—*Castula doubledayi* Newm. Fig. 20.—*Papilio aegeus* Don. cua., Cubito-anal cross-vein.

On the other hand, M2 arises from midway between M1 and M3 or is approximated to M1 in the Bombycoidea, Sphingoidea, Uranoidea, and Geometroidea (except in the genus *Microdes* of the Larentiadae).

A GENERAL SURVEY.

Having completed our examination of various details of neurulation, let us now stand back and take a general view of the position attained. We commenced by dividing the Lepidoptera into two suborders of very unequal size, the Homoneura and Heteroneura. This division, we believe, is now generally accepted. We divided the latter into two divisions, the Asthenochorda and Sthenochorda. This is a new conception, but appears securely based on two different lines of evolution. The distinction between them is clear and unambiguous, though the primitive representatives of both are derivable from a common stem, for which I have proposed the name Protocossidae, denoting a hypothetical family combining the primitive neurulation of the Cossidae with the primitive mouth-parts of the earliest Tineoidea. We then considered more in detail the position of the Rhopalocera. It was evident that though these appeared more nearly allied to the other superfamilies of the Asthenochorda than to the Sthenochorda, they differed from the former in some important characters, which appeared amply sufficient to justify their separation as a distinct subdivision. We found no sufficient reason to exclude the Hesperidae from the Rhopalocera, though it forms a very distinct superfamily, specialized in some respects, but more primitive in others. It now remains to make a more detailed examination of the families and superfamilies. As to the former there appears to be (with a few exceptions) general agreement; but as to the latter no such agreement has yet been obtained. In the classification here proposed the superfamilies are based on structural characters and differ much in extent. Many of them consist of a single family. Others are dominant groups and contain many families.

THE SUPERFAMILIES OF THE RHOPALOCERA.

From all the other Rhopalocera the Hesperidae differ in their simple tortriciform neurulation (Fig. 17), their broad head, and usually their peculiar hooked antennae. To this may be added the usual presence of middle spurs in the posterior tibiae, the presence of a frenulum and retinaculum in *Euschemon* (Fig. 28), and the curious backward direction of the humeral veinlet in the hindwing, which occurs also in *Eurycus* of the Papilionidae (Figs. 22 and 23). Taking all these characters together, with special stress on the first, I agree with Meyrick in admitting the superfamily Hesperoidea, but I think he goes too far in writing (1927) that they have no connection with the rest of the Rhopalocera, "the resemblance being in part analogical and the differences profound". On the contrary, the stalking of R3 and R4 of the forewings, which is present in all the latter, appears to be strictly analogous to their stalking in the great majority of the Pyraloidea. There is a very strong probability that, as in that superfamily, the stalking is a modification of a previous tortriciform condition. If this be admitted there seems to be no reason to consider the Hesperoidea as other than a specialized offshoot from the primitive rhopalocerous stem.

I divide the remaining families into the Papilionoidea and Nymphaloidea. The former shows the following peculiarities: (1) There is a cubito-anal cross-vein in the forewings (Fig. 20). (2) The vein 2A in the forewings runs independently to the dorsal margin. (3) The subcostal and first radial arise independently from the base of the hindwings and fuse to form a precostal cell. (4) One anal vein has been lost in the hindwings. Three of these characters are peculiar to the Papilionidae; the third is, so far as I know, present also only in the genus *Elymnias* of the Nymphalidae, and not elsewhere in the Asthenochorda, though it is found in several groups of the Sthenochorda.

Of the Nymphaloidea three families are contained in the European and Australian faunas, the Lycaenidae, Pieridae and Nymphalidae. The first two present some similarity, but it is doubtful whether this is not due merely to convergence. It is certainly remarkable that the Pieridae and Papilionidae, so different in the imago, are so similar in their pupae. In these two families the angular pupa, girdled with a silken thread and with head uppermost, is a fixed character. The suspension with the head

downwards without a girdle in the Nymphalidae may, I think, be a later development from this. It is difficult to see how the nymphalid position could have been changed into that of the Pieridae and Papilionidae, but the contrary change is not difficult to understand. In neurational characters the Lycaenidae, which have lost the precostal spur in the hindwing, and usually one vein of the forewing, are probably the most recent. This is confirmed by their small size (an instance of the asthenogenesis so operative in the Lepidoptera), their present dominance in number of species, and the intimate association of many species with ants.

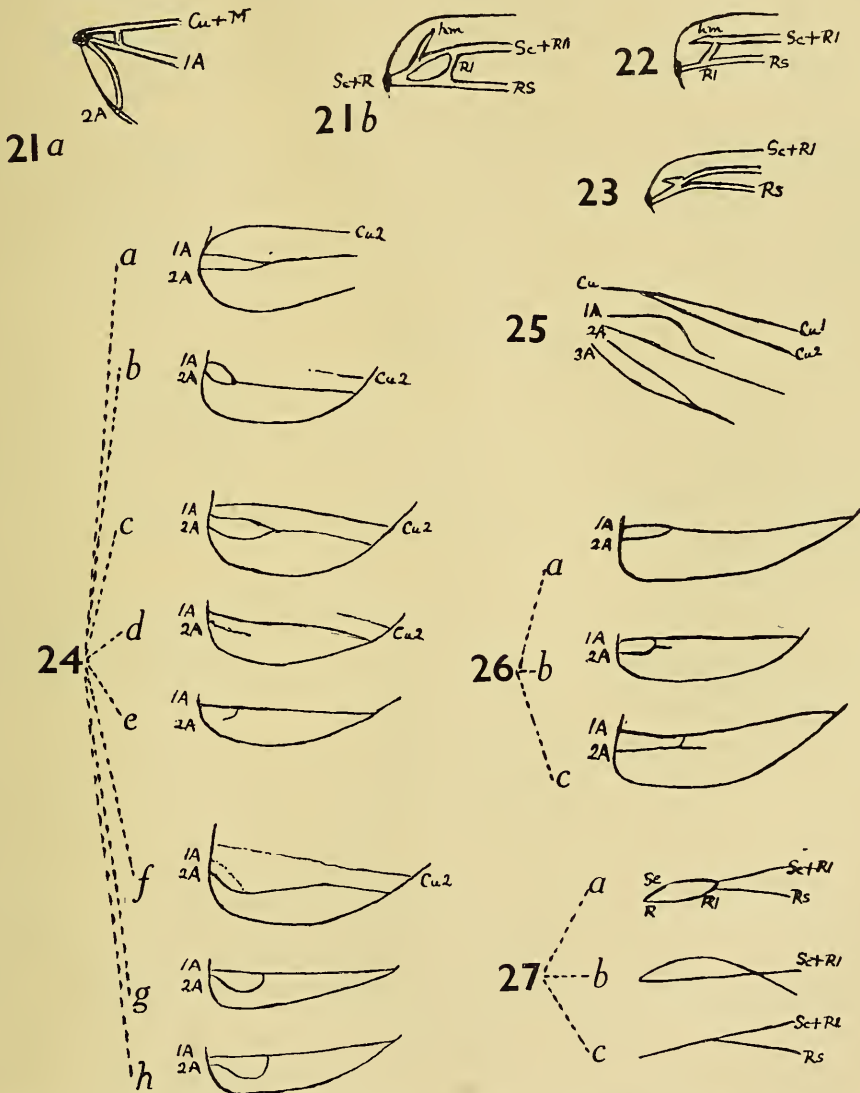


Fig. 21a.—*Papilio aegeus*. Parts of bases of fore- and hindwings. Figs. 21b-23.—Part of base of hindwings. Fig. 21b.—*Papilio aegeus*. Fig. 22.—*Eurycyus cressida* Fab. Fig. 23.—*Hasora haslia* Swin. Fig. 24.—Anal veins of hindwings. a. *Macrocyttara expressa* Luc. b. *Tortrix musculana* Hb. c. *Carcina quercana* Fab. d. *Monopis rusticella* Hb. e. *Tinea corticella* Curt. f. *Endrosis lacteella* Schiff. Fig. 25.—*Laspeyresia pomonella* Lin. Pupal tracheation of part of hindwing (Tillyard). Fig. 26.—Anal veins of hindwings. a. *Biston betularius* Lin. c. *Othreis materna* Lin. Fig. 27.—Subcostal and radial veins of hindwings. a. *Stilpnolia salicis* Lin. b. *Porthesia chrysorrhoea* Lin. c. *Tyria jacobaeae* Lin.

THE SUPERFAMILIES OF THE MICROPTILA.

SUPERFAMILY ZYGAENOIDEA.

This was probably at one time a much more extensive group than it is at present, and is now represented by fragments only of its former extent. There is no trace of a chorda in the imaginal wing, but a median vein is present in both wings, usually a single vein, rarely forked in the forewing, still more rarely in the hindwing. Figure 29 shows a primitive tortriciform neuration; Figure 30 is a more specialized form with stalking of the forewing radials, together with stalking of M2 and M3 in the forewing, but is more primitive in having intracellular forked medians. In this family, Cu2 is present in both wings, and in the hindwing R1 arises from the middle, or beyond the middle, of the cell and is very short, the subcostal being closely approximated to the cell. In some instances this short vein is replaced by an anastomosis.

SUPERFAMILY PYRALIDOIDEA.

This large and well-characterized superfamily is one of the dominant groups of the Lepidoptera. It contains six families, which have been clearly defined by Meyrick and Hampson. The tortriciform neuration, which has been shown to be characteristic of the Asthenochorda, occurs in most of the Thyrididae (Fig. 18) and in one genus of the Pyraustidae. No trace of the chorda or median is present in the imaginal forewing, but Tillyard found that they were present in the pupal forewing of *Morova*, the New Zealand representative of the Thyrididae. In the great majority, R3 and R4 of the forewing are stalked, but sometimes coincident in the Phycitidae. M2 is approximated to M3 in both wings. Cu2 is absent in the forewing but, except in the Thyrididae, present in the hindwing, which has two anal veins, one being the conjoint 1A + 2A, the other 3A. A distinctive character is the approximation or anastomosis of the radial sector to the subcostal beyond the cell of the hindwing. The former occurs in the Thyrididae and some genera of the Pyralidae; but in all other cases these veins anastomose almost immediately after the origin of the radial sector. Except in the Thyrididae and a section of the Pyralidae, the maxillary palpi are sufficiently developed to be easily recognizable.

As a representative I figure one of the Pyraustidae (Fig. 33). The boat-shaped loop formed by 2A in the forewing is well shown. This appears to be peculiar to that family, but in most of its genera 2A has disappeared. A simple anal is the rule in the other families; a small basal V-loop is rarely present. The anastomosis of S and Rs in the hindwing is characteristic. The more primitive condition, in which these veins are merely approximated, is shown in Figures 31 and 32.

The Tineodidae is a small family related to extinct forms of Pyraustidae, from which the family differs in M2 of the hindwing arising from the middle of the cell well separate from M3 (only in *Tanycnema* are these veins somewhat approximated); M1 may be either connate or separate from Rs, which is either approximated to, or anastomoses with, S beyond the cell. In the forewing all veins from the cell may be separate or R3 and R4 may be stalked. Except in *Tanycnema* the maxillary palpi are distinct. *Oxychirota* is an anomalous genus with extremely narrow wings, R2, R3, R4 and R5 being stalked. *Coenoloba* is unique in having both wings 2-cleft. The forewing has Cu1a and Cu1b stalked; and R1, R2, R3 and R4 stalked; the hindwing Cu1a and Cu1b stalked, M1 and Rs stalked; and Rs anastomosing with the subcostal. The maxillary palpi are rather large and triangularly scaled.

The small number of existing genera (all but one Australian) so far known, together with their extraordinary diversity, points to this being an archaic group, which has suffered much extinction, leaving only a few survivors.

SUPERFAMILY PTEROPHOROIDEA.

This group is remarkable for the extensive fissuring usual in both wings. In the forewing the Pterophoridae are 2-cleft (rarely three- or four-cleft), in the hindwing usually 3-cleft. Fortunately there are three genera in which the wings are not cleft, and these are the best guide for the phylogeny. In *Agdistis* (Fig. 34) the neuration of the forewing is archaic, all the veins from the cell of the forewing arise separately, while

Cu2 is developed in both wings. The fusion of M2 and M3 of the hindwings is a specialization. The presence of Cu2 in both wings seems to be an invariable character in the Pterophoridae, and R3 and R4 may be stalked or coincident (Fig. 45). In some genera, such as *Alucita*, the neuration is much reduced. The maxillary palpi are always obsolete. A curious character is the presence of a double row of short spine-like dark scales on the lower margin of the cell beneath. There is probably real but rather remote affinity between the Pterophoridae and the Tineodidae.

In his Revised Handbook, Meyrick removed the Orneodidae to the Tineoidea, but later he restored them to the place they occupied in his first Handbook, immediately

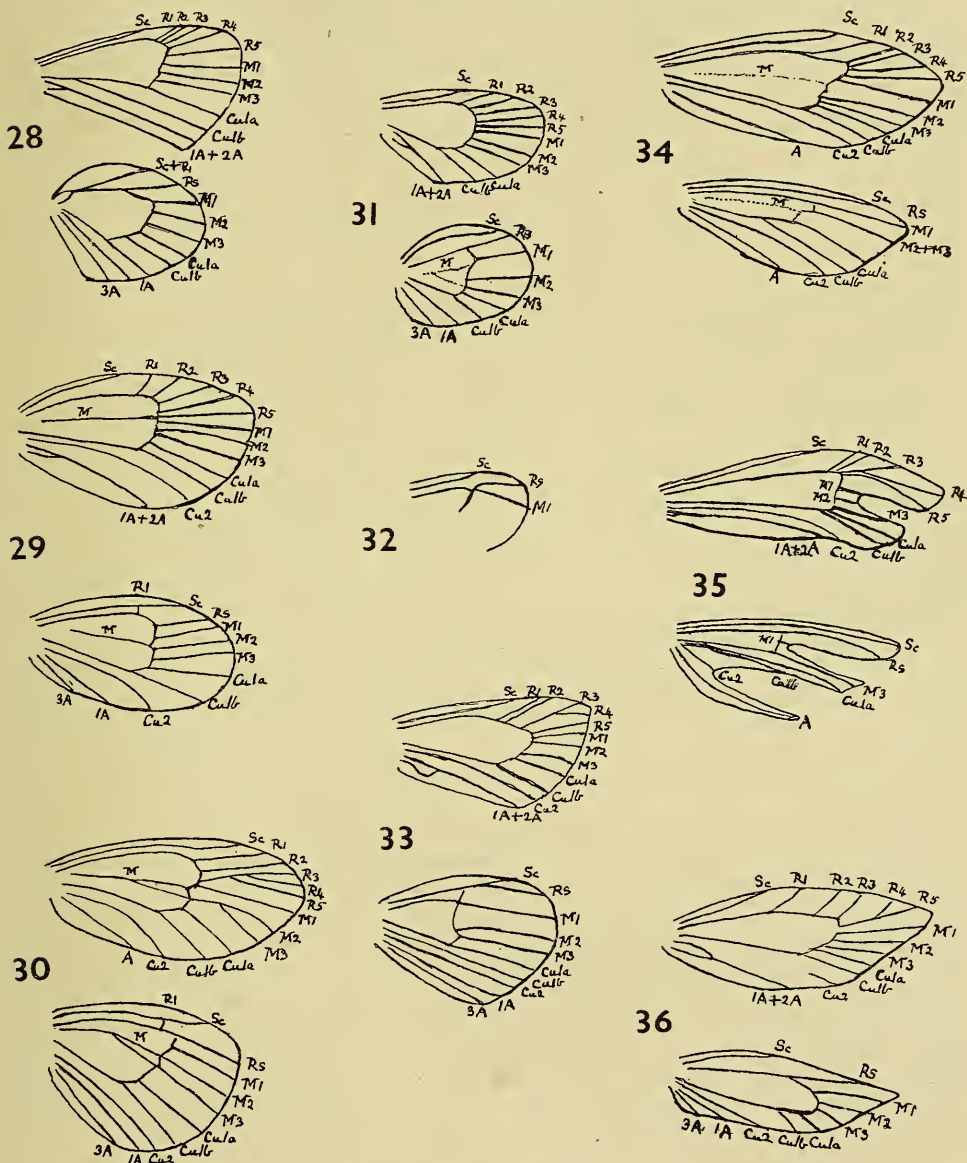


Fig. 28.—*Euschemon rafflesia* Macl. Fig. 29.—*Procris statites* Lin. Fig. 30.—*Chelura bifasciata* Hmps. (after Hampson). Fig. 31.—*Striglina irias* Meyr. Fig. 32.—*Epipaschia atribasalis* Warr. Part of hindwing. Fig. 33.—*Mecyna ornithopteralis* Gn. Fig. 34.—*Agdistis benneti* Curt. (after Meyrick). Fig. 35.—*Stenoptilia pterodactyla* Lin. (after Meyrick). Fig. 36.—*Mompha fulvescens* Haw. (after Meyrick).

following the Pterophoridae. They are a small group of four genera, three of which have both wings 6-cleft; the other has the forewing 6-cleft and the hindwing 7-cleft. In *Orneodes* the wings are fissured nearly to the base and each segment is occupied by a single vein.

The superfamily Pterophoroidea does not have Rs of the hindwing more closely approximated to the subcostal beyond the end than before the end of the cell. It also differs from the Pyraloidea by the presence of Cu2 in the forewing.

SUPERFAMILY TINEOIDEA.

This immense superfamily comprises more than one-third of the known Lepidoptera, and when the world fauna is better known should approach one-half. It contains the most primitive of the Heteroneura, for its only rival, the superfamily Cossoidea, is less primitive in its mouth-parts. Among the primitive characters that it occasionally presents are (1) the 5-jointed folded maxillary palpi; (2) the occasional presence of the chorda, seldom strongly developed, in the forewing (Figs. 12 and 13); (3) occasionally a weak or vestigial median, seldom forked, in the cell of both wings; (4) the second cubital more or less developed in both wings; (5) the first and second anals forming a basal loop in both wings; and (6) the third anal in the hindwings. These characters are rarely combined in one genus. The long folded maxillary palpi are found only in the Nepticulidae and the Tineidae (*sensu lato*), but in many of the latter family they are short or absent. The chorda and median veins in the cell have disappeared in the great majority of the genera, and the resultant tortriciform neurulation has been lost in a great many by stalking. It is noteworthy that the first radial veins to be stalked are almost always R4 and R5, not R3 and R4 as in the preceding superfamilies.

These changes in neurulation are small compared with those that have occurred in a great number of genera, which have undergone asthenogenesis to such an extent that it is sometimes difficult to recognize which veins have been retained. From this aspect the Tineoidea contains some of the most specialized of the Lepidoptera, small, narrow-winged, and often minute. In the accompanying figures (Figs. 40-46) it will be observed that, except in *Opostega* (Fig. 45), the forewings have their neurulation relatively slightly reduced. The hindwings have undergone greater reduction, the loss affecting mostly the median veins. Cu2 has been lost in some; one has lost a branch of the first cubital; but all have retained 1A and 3A.

I can see no justification for the separation of the Tortricoidea as a separate superfamily. This opinion was expressed many years back by Walsingham. Meyrick himself states in his Revised Handbook (p. 25) that "the Tortricina originated from the Glyphipterygidae, the Eucosmidae being the basic family, and its most primitive genus, *Laspeyresia* (with its allies), approaches certain special forms of the Glyphipterygidae in all structural and superficial respects so closely, that it is difficult to draw any line between them".

Not only is the Tineoidea the most dominant superfamily of the Lepidoptera at the present time, but it appears still to be undergoing active evolution. The number of known species is overwhelming, and is being increased every year, while in many regions this part of their fauna has hitherto hardly been touched. At the date of the publication of the Revised Handbook, Meyrick recognized 33 families, of which 21 were British, in his Tineina (excluding the Tortricina). These he divided into seven "tribes" with names ending in -oidea. As this suffix has been generally used by entomologists to denote superfamilies, this usage appears inadmissible, and some other form of nomenclature seems to be needed. The immense amount of work done by Meyrick in this group, and his great experience, should make us very careful in making any change in his classification. His nomenclature may, I think, be varied by regarding his "tribes" as families and his families as subfamilies. For instance, the Tortricidae may be divided into Phalonianae, Tortricinae, Eucosminae, etc., and the Gelechiidae into Gelechiinae, Oecophorinae, etc. I doubt whether all his groups are equally valid, but I shall propose only one major alteration. Meyrick regarded the Cosmopterigidae as developed by asthenogenesis in his Gelechioidea, the Elachistidae, Douglassiadae and Sythidae in his Hyponomeutoidea, and the Coleophoridae in his Plutelloidea.

Convergence through asthenogenesis is common in the Lepidoptera, and his judgment may be correct. But he seems to me to fail in this instance to give clear reasons for this decision. In view of the close correspondence in neurulation and other characters of these five groups, I propose, but with some diffidence, to consider them as subfamilies of the Elachistidae.

The following list, which includes only groups represented in the British and Australian faunas, includes 9 families and 30 subfamilies.

1. Elachistidae with the five families already mentioned.

2. Gelechiadae with seven subfamilies, Gelechiinae, Xyloryctinae, Blastobasinae, Oecophorinae, Thalamarchellinae, Amphitherinae and Hyponomeutinae.

This is a very extensive group; the Gelechiinae containing over 3,500 and the Oecophorinae over 3,000 known species. On the other hand, only 8 of the Amphitherinae and 4 of the Thalamarchellinae have been described. This great disparity does not invalidate the status of these groups, which is not concerned with the number of species in each group, but with the conception of the evolutionary stems, as deduced from structural characters, on which they have developed. Furthermore, the affinities of these stems depend entirely on their most primitive genera, and are in no way affected by their specialized genera, however far these may have diverged.

3. Tortricidae with four subfamilies, Phaloninae, Tortricinae, Eucosminae and Chlidanotinae.

All these are closely allied, especially the second and third, which are separated by only one character, not of great morphological value and not absolutely constant.

4. Copromorphidae with two subfamilies, Carposininae and Copromorphinae.

5. Aegeriadae.

6. Glyphipterygidae with three subfamilies, Heliozelinae, Heliodininae and Glyphipteryginae.

I am somewhat doubtful about the position of the first two subfamilies.

7. Plutellidae with three subfamilies, Gracilariinae, Epermeninae and Plutellinae.

8. Nepticulidae.

As Meyrick points out, the neurulation of this family is peculiar in the absence of the cell in both wings. In the forewing this is associated with a basal coalescence of the median with either the radial or cubital or both (Fig. 47). This is a structure not found elsewhere in the Lepidoptera, and Meyrick has suggested that the family arose by a separate stem from the Micropterygoidea. This seems to me unlikely. The family Nepticulidae has a normal frenulum, and the palpi conform to the tineoid type. I think it is probable that it is an ancient offshoot from the Tineidae, and is not entitled to more than family status.

9. Tineidae with seven subfamilies, Epipyropinae, Cyclotorninae, Opisteginae, Lyonetinae, Tineinae, Lamproninae and Adelinae.

This group, together with the Nepticulidae, contains all the Heteroneura, which have retained the primitive long five-jointed folded maxillary palpi. It includes also many in which the maxillary palpi are short or absent. The Epipyropinae and Cyclotorninae are small groups whose larvae have become specialized in their habits. In both, the neurulation is of primitive tineoid character. The former have lost maxillary and labial palpi and tibial spurs; and their larvae are parasitic on Homoptera. The latter have lost maxillary palpi, their labial palpi are very short, straight, stout and obtuse, but the tibial spurs are well developed; the larvae spend their later stages in ants' nests. The Opisteginae, with their extremely degraded neurulation, not explicable by mere reduction in size, appear to me to be more entitled to subfamily rank than many recognized subfamilies. Compare the neurulation of *Opistega* (Fig. 45) with that of *Leucoptera* (Fig. 46).

THE SUPERFAMILIES OF THE STENOCHORDA.

SUPERFAMILY BOMBYCOIDEA.

Tongue, palpi and frenulum present or absent. No median vein in cell of both wings. Forewings without areole except in Cymatophoridae and Notodontidae; R₃, R₄

and R5 usually stalked, M2 from middle or above middle of cell, Cu2 absent (except sometimes in Bombycidae). Hindwings with Cu2 and A3 present or absent.

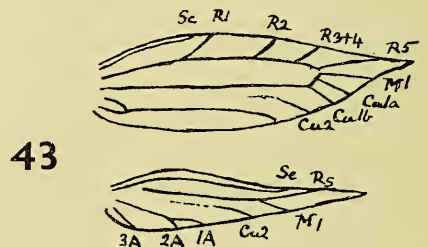
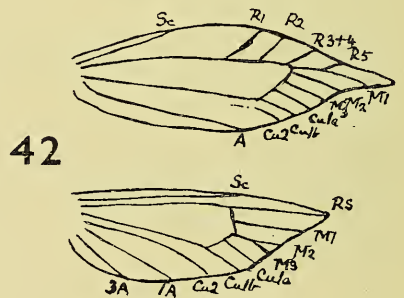
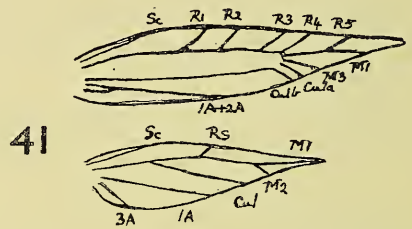
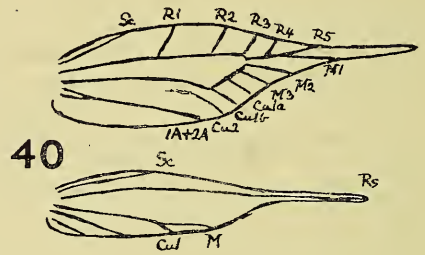
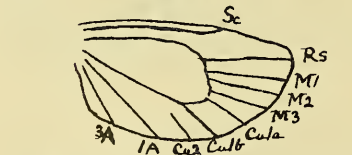
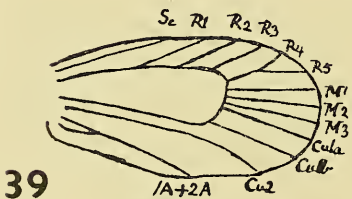
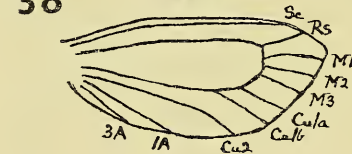
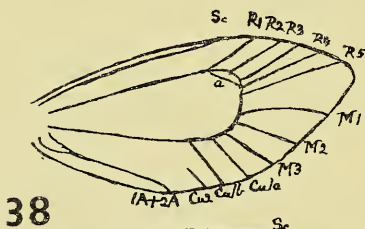
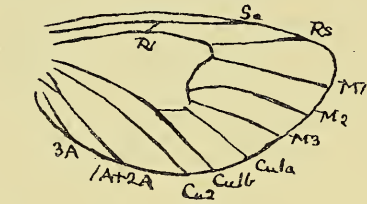
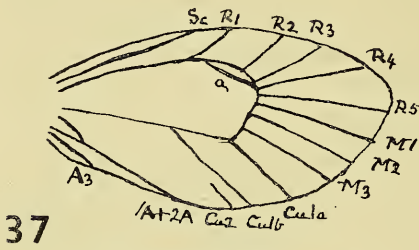


Fig. 37.—*Argyroproct salicella* Lin. Fig. 38.—*Moerarchis australasiella* Don. Fig. 39.—*Thalamarchella alveola* Feld. Fig. 40.—*Cosmopteryx druryella* Zel. (after Meyrick). Fig. 41.—*Douglasia oenostomella* Stn. (after Meyrick). Fig. 42.—*Scythris fuscoaenea* Haw. (after Meyrick). Fig. 43.—*Coleophora onosmella* Brahm. (after Meyrick).

There are six families, which form a natural group, though with some diversity of structure. For instance, the frenulum is absent in the Saturniadae and Brahmaeidae, present in the Cymatophoridae and Notodontidae, while in the Bombycidae it may be present or absent. Though the presence or absence of the frenulum is usually a family character, too much weight has been given to it. In the Geometridae every stage between a well-developed, weakly-developed and absent frenulum is found within a very clearly defined family, and *Euschemon* must be placed in the Hesperidae, in spite of its strong frenulum in the male.

The family Saturniadae is the most specialized and is remarkable for the combination of large size with reduced neurulation. Tillyard's examination of the pupal wing of *Antheraea* showed that even in that stage there was no areole, also that in the forewing the radial was four-branched and the median two-branched. The tongue and frenulum are absent. The palpi are short or obsolete, and the same applies to the tibial spurs. Middle spurs on the posterior tibiae are never developed. The forewings have no areole, M2 is absent, R2 and R3 are coincident. In the hindwings the subcostal diverges widely from Rs. R1 is absent, Rs arises much before the angle of the cell, and Cu2 is absent. In *Attacus* the discocellulars are absent leaving the cell open in both wings (Fig. 48).

In this family I include the genera, which have been known as Citheroniadae. The Saturniadae includes some of the largest of the Lepidoptera, an order in which size, unless compensated by some other factor, is a hindrance to survival. The family appears to have become over-specialized, and as a consequence, the species are not numerous, probably less so now than in the more or less remote past. These remarks apply also to the Brahmaeidae, and to a less degree to the other three families.

In the Bombycidae (in which I include the Eupterotidae) the tongue is absent; the palpi short or obsolete; the frenulum present or absent (in *Bombyx* it is rudimentary). In the forewing R2, R3, R4 and R5 are stalked or R2 is absent, Cu2 is rarely present, and there is no areole. In the hindwing the subcostal diverges from the cell near the base, 3A is present, but Cu2 is rarely developed (Figs. 49 and 50).

The Brahmaeidae (Hampson, 1892) consists of only one genus and a few species in the Oriental region. The tongue is present. The palpi large rounded and upturned. The frenulum absent. In the forewing M2 arises from the upper angle of the cell. In the hindwing the subcostal is approximated to the radial sector beyond the cell, which is short, M2 arises from near the upper angle of the cell, 3A is absent and Cu2 is absent in both wings.

In the Cymatophoridae tongue and frenulum are present. In the forewing there is a long, narrow areole, which may be present or lost by dissociation within the same species. In the hindwing Rs arises before the angle and is curved and approximated to the subcostal beyond the cell, 3A is present in the hindwing, but Cu2 is absent in both wings.

In the Notodontidae the tongue may be present or absent. The frenulum is present. The forewing may or may not have an areole. In the hindwing the subcostal is usually approximated to the cell, M2 is weakly developed or seldom absent and 3A is present. This is the most primitive of the six families. There are two subfamilies. The Cnethocampinae represents an early offshoot from the notodontid stem, differing from the Notodontinae by the tongue being always absent, the palpi being small or obsolete, the abdomen having a large apical tuft, and the hindwings with the subcostal sometimes widely separate from the cell, but more often approximated at one-fourth and sometimes further (Fig. 52). In the Notodontinae the tongue may be well developed, weakly developed, or absent; the palpi are always present; and the subcostal of the hindwing is usually approximated to the cell to near its end, always to its middle, rarely connected or anastomosing (Fig. 51).

SUPERFAMILY GEOMETROIDEA.

Tongue usually well developed. Frenulum present except in some Geometridae. Forewing often with areole, but no median in cell of either wing; R1 often anastomosing with R2, R4 and R5 stalked, R3 often stalked with them, Cu2 absent, M2 from middle or

above middle of cell. Hindwing with Sc bent at base into a humeral angle, Cu2 absent, 3A present or absent. In *Microdes* (Larentiadae) M2 of forewing arises below middle.

This is a large and dominant superfamily in the Sthenochorda, second only to the Noctuoidea. It contains five families, the Larentiadae, Sterrhidae, Geometridae, Boarmiadae and Oenochromidae. The distinctions between the families have been so

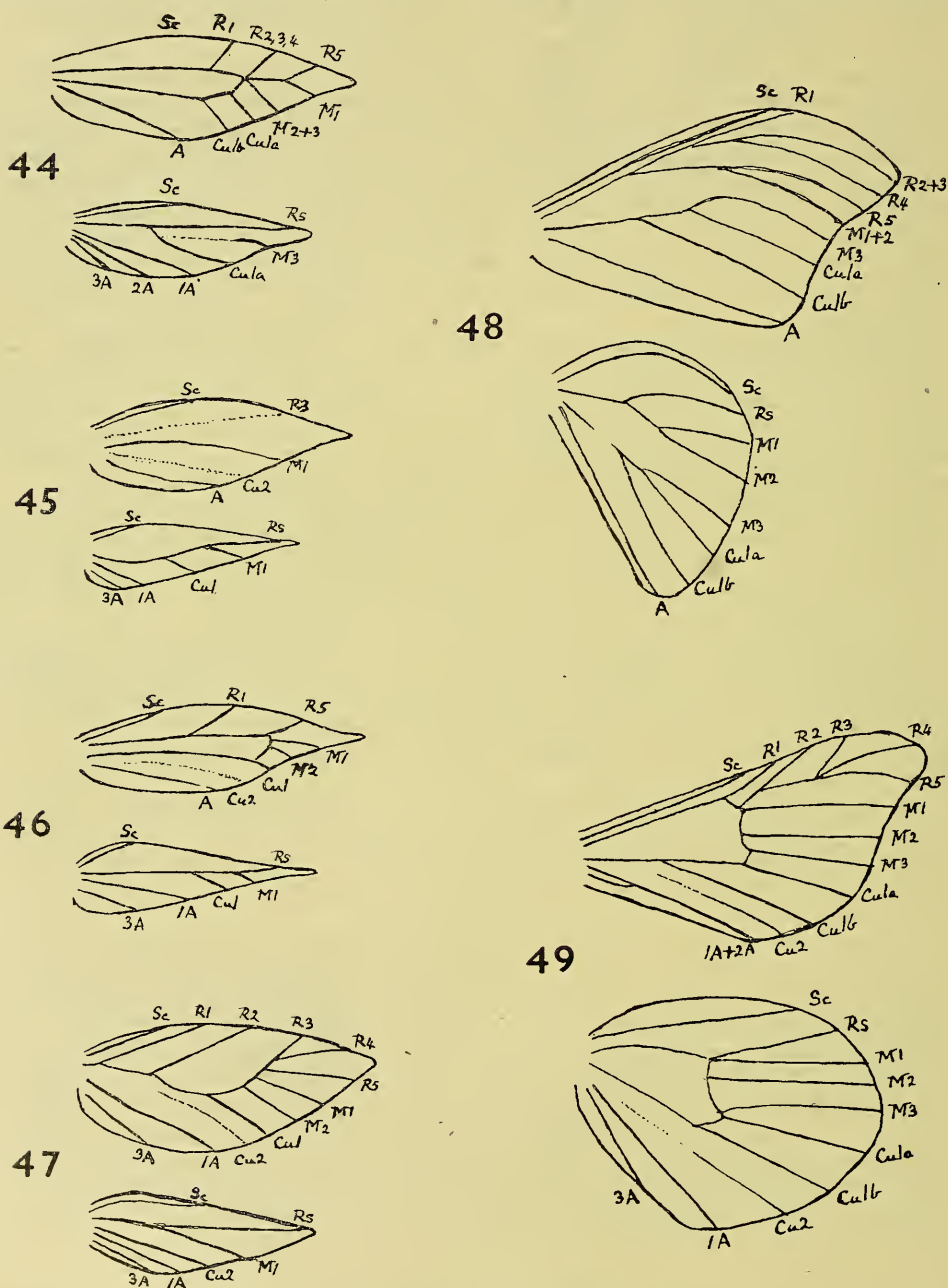


Fig. 44.—*Heliozela stannella* F.v.R. (after Meyrick). Fig. 45.—*Opostega crepusculella* Zel. (after Meyrick). Fig. 46.—*Leucoptera laburnella* Stn. (after Meyrick). Fig. 47.—*Scoliaula quadrimaculella* Boh. (after Meyrick). Fig. 48.—*Attacus dohertyi* Roths. Fig. 49.—*Bombyx mori* Lin. (after Comstock).

well given by Meyrick and Prout that it is not necessary to recapitulate them here. The first four are clearly defined; the Oenochromidae are fewer in species, but show more variation in structure, varying from primitive to specialized forms, which have developed along several different lines. These appear to represent early offshoots from the primitive stem of the Geometroidea; offshoots which have suffered much extinction or never developed to any large extent. In Australia, owing to less competition from the other families, some of these offshoots have developed to a moderate extent. Elsewhere the surviving genera and species are few. From this generalized family the other families have developed. It will be interesting to follow this development in the radial veins of the forewing. We commence with *Xenogenes* (Fig. 53a) of the Oenochromidae with its primitive areole and R1 arising separately. In *Epidesmia* R1 anastomoses with the areole, forming what has been conveniently named a double areole. Strictly speaking, however, the posterior of the twin cells is the areole, the anterior is a new formation, which we may call a pseudoareole. In the Larentiadae the areole persists; the pseudoareole also often persists as in *Cidaria*, but frequently it is lost by coalescence, thus restoring the single areole; in a few genera of this family the single areole has also been lost by coalescence. In *Acodia pauper* a curious condition occurs, in which the areole has disappeared in most, but not all, specimens by failure of its posterior wall (represented in the figure by a dotted line) to chitinize. The same abnormal neurulation is developed as a rare aberration in other species, in which the areole is normally intact (see Figs. 53, a-h).

The family Sterrhidae has developed along a different line. Here both areole and pseudoareole are present in *Autanepsia* and *Organopoda*. More frequently only a single cell, which is the pseudoareole, is developed, and the radial veins arise on a common stalk from well before the end of the cell as in *Brachycola*. The same transformation has occurred in the larentiad genus *Cataclysmes*. It can hardly be doubted that this form of neurulation is also the result of a failure of the posterior wall of the areole to chitinize. In a few genera this pseudoareole is very small and sometimes lost by coalescence.

In one section of the Oenochromidae the areole is very long and narrow, and its very short posterior wall may either persist or disappear (by failure to chitinize) in the same species. In the family Boarmiadae, which has an areole in its earlier genera, it has disappeared in most. This disappearance of the areole by dissociation is actually the same process as recorded in the last paragraph, but is less striking, because of the smallness of the apparent change, and because the close approximation of the veins separated indicates that the loss of the connecting bar is of no mechanical importance. In the figure of a species of *Cleora* (Fig. 54) the resemblance of the neurulation to that of an *Oenochroma* (Fig. 53h), in which the areole has been lost, is obvious. This is not so obvious in the figure of a species of *Boarmia* (Fig. 55), but in that and many other genera it has been obscured by great variability even in the same species. R1 may be stalked or coincident with R2, their common stalk, or R1 may be connected or anastomose with the subcostal, R2 may anastomose with R3, and other variations are possible.

In the Geometridae the areole is never developed. The neurulation of their earlier genera, except for the presence of M2 in the hindwing, closely resembles that so often found in the Boarmiadae. We may say that the family Geometridae seems to begin where the Boarmiadae leaves off. Probably, however, the former arose separately from that section of the Oenochromidae, in which R1 anastomoses first with the subcostal and then with R2. Compare the forewing neurulations of *Eumelea* (Fig. 57) and *Crypsiphona* (Fig. 56).

Meyrick included the Bombycoidea with the Geometroidea in a single superfamily under the name Notodontina. Certainly if the neurulation were our only guide, the family Notodontidae comes very near the Oenochromidae; the only constant difference being the humeral angle all-present at the base of the subcostal of the hindwing in the Geometroidea. To this there is no exception, now that *Diceratucha* (Fig. 59) formerly referred to the Oenochromidae, has been found to be one of the Notodontidae. This difference alone would not justify the separation of the superfamilies, but Prout (1910) has pointed out a more important anatomical difference. It relates to the morphology

of the basal cavity and tympanum in the second abdominal segment and its relation to the first segment with its spiracle. (For further details regarding the Oenochromidae see Turner, 1929.)

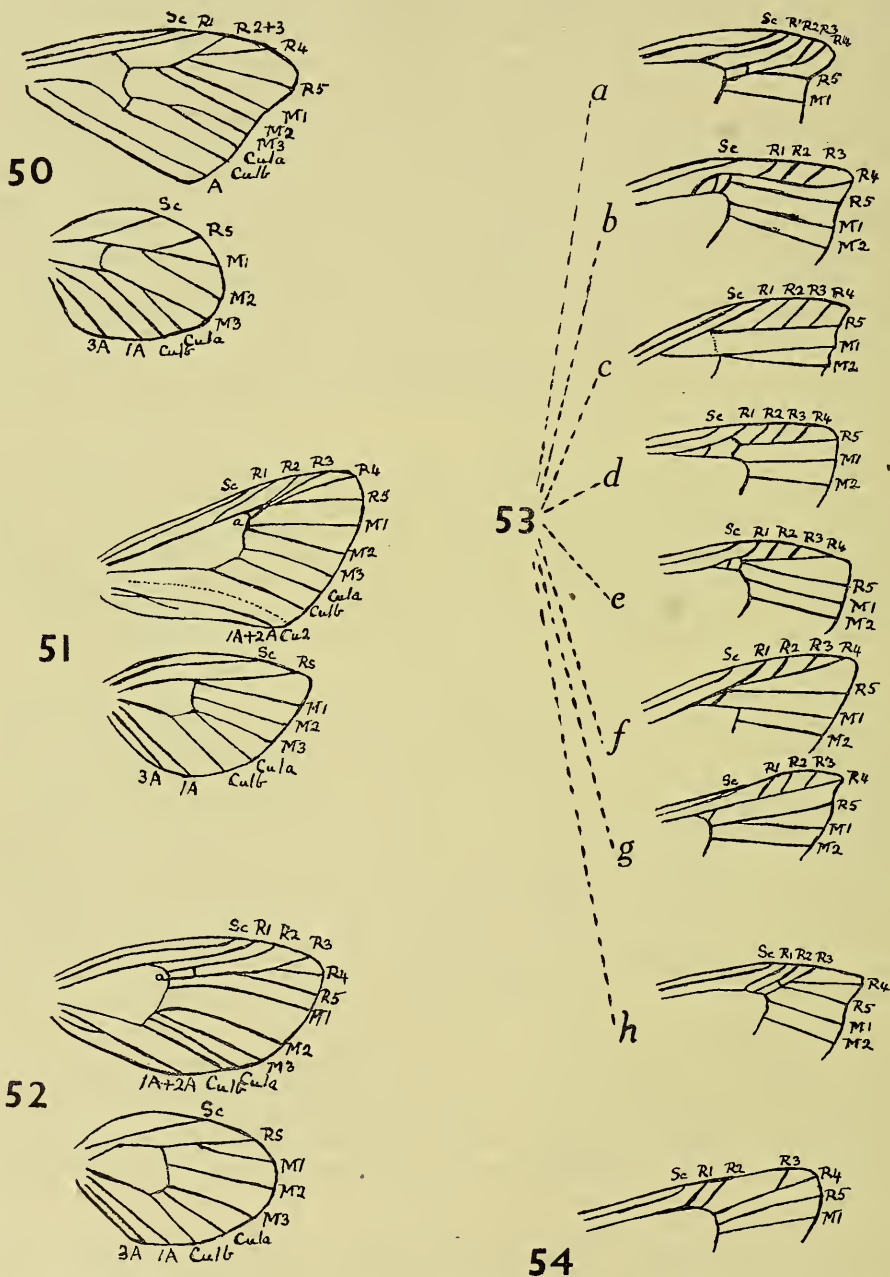


Fig. 50.—*Panacela nyctopa* Turn. Fig. 51.—*Cerura vinula* Lin. (after Meyrick). Fig. 52.—*Ochrogaster contraria* Wlk. Fig. 53.—Apical part of forewing in eight genera of Geometroidea showing variations in the structure of the areole. a. *Xenogenes eustrotiodes* Prout. b. *Epidesmia hypenaria* Gn. c. *Acodia pauper* Rosen. d. *Autanepsia poliodesma* Turn. e. *Organopoda olivescens* Warr. f. *Brachycola porphyropis* Meyr. g. *Cataclysta virgata* Roff. (after Meyrick). h. *Oenochroma vinaria* Gn. Fig. 54.—*Cleora illustraria* Wlk.

SUPERFAMILY URANOIDEA.

Tongue present. Thorax and abdomen slender. No median vein present in cell of either wing. Forewing without areole; R1 separate or arising separately and often running into the subcostal; R3 and R4 stalked, R2 stalked with them or separate, rarely absent, R5 widely separate from R4, connate or more often stalked with M1, and M2 from middle or from above middle of cell. Hindwing with R1 absent, subcostal separate, M2 from middle or from above middle of cell; and Cu2 absent in both wings (Figs. 60-62).

This superfamily, which is of no great extent, consists of two distinct families. Its most striking character is the wide separation of R5 from R4, R5 being connate or stalked with M1.

The Uraniadae is a small and specialized group comprising some large day-flying species, though the majority are of more moderate size. In them the frenulum is absent; in the forewing 1A and 2A form a basal fork; in the hindwing 3A is absent.

Members of the family Epiplemidæ are of small size and inconspicuous coloration. They have retained the frenulum; there is no basal anal fork; in the hindwing 3A is present (Figs. 61, 62).

SUPERFAMILY SPHINGOIDEA.

This group consists of a single isolated wide-ranging family. The species are of large or at least of moderate size. The thorax and abdomen are robust. The tongue is usually well developed and sometimes extremely long, but in a few genera, short and weak. The palpi are peculiar, being usually large, broad, closely applied to the head, and with a small or minute terminal joint often hidden by scales. The antennae are usually rather short or at most of moderate length, subcylindrical, often thickened towards apex, but seldom clubbed, and they have frequently an apical hook. In the wings the areole is never present and there are no median veins in the cell of either wing. In the forewing R1 arises from the cell beyond the middle, R2 is stalked or coincident with R3, R4 and R5 are stalked, M1 arises from near the upper angle of the cell, or is stalked with R4 and R5, M2 is always nearer M3 than M1, usually it arises from below the middle of the cell, but is never closely approximated to M3, Cu2 is absent and 1A and 2A are basally forked (Figs. 63, 64). In the hindwing R1 is always present, Rs is always approximated to the subcostal beyond the cell, M2 arises from the middle of the cell or from slightly above or below, Cu2 is absent, but 3A is present.

The neururation in the Sphingidae varies very little, and is consequently of little value in the internal classification of the family. Rothschild and Jordan have studied with much thoroughness (1903) other anatomical features, which they have employed for this purpose. The approximately median origin of M2 of the forewing is a generalized character, being intermediate in its position to that in the preceding and following superfamilies.

SUPERFAMILY NOCTUOIDEA.

The maxillary palpi are rudimentary or absent (except in *Hyblaea*). There is no median vein in the cell of either wing and Cu2 is absent in both wings. The frenulum is present (only in the male in the Anthelidae). In the forewing M2 is approximated or connate with M3 at its origin. In the hindwing the subcostal usually anastomoses with the cell, and 3A is present (but often absent in the Syntomidae).

This is by far the largest superfamily in the Sthenochorda. It is a natural group of six families. These show a wide range of structural variation. The family Syntomidae is a specialized development of the Arctiidae, and lacks some of the more primitive characters that are present in some or all of the genera of the other five families. The areole is never present. The hindwing is always small and has undergone more or less reduction in the number of its veins (Figs. 65, 66). The subcostal is always completely fused with the cell and radial sector throughout, and may therefore be said to be absent. In many genera one or two other veins have been lost, the missing veins not being the same in all of them; 3A is also often absent.

The family Arctiidae has preserved the areole in its more primitive genera. When absent it has disappeared by coalescence, except in a small group of genera in which it

has disappeared by dissociation (Fig. 19). In the hindwing the subcostal has completely fused with the base of the cell and this fusion extends usually to the middle of the cell or even beyond, and in a few cases includes the base of the radial sector; M2 is approximated, connate, stalked, or coincident with M3 (Fig. 67). The retinaculum is nearly always bar-shaped; and the palpi are short. There is great variety in the neuration owing to the frequent stalking or coincidence of veins in either or both wings.

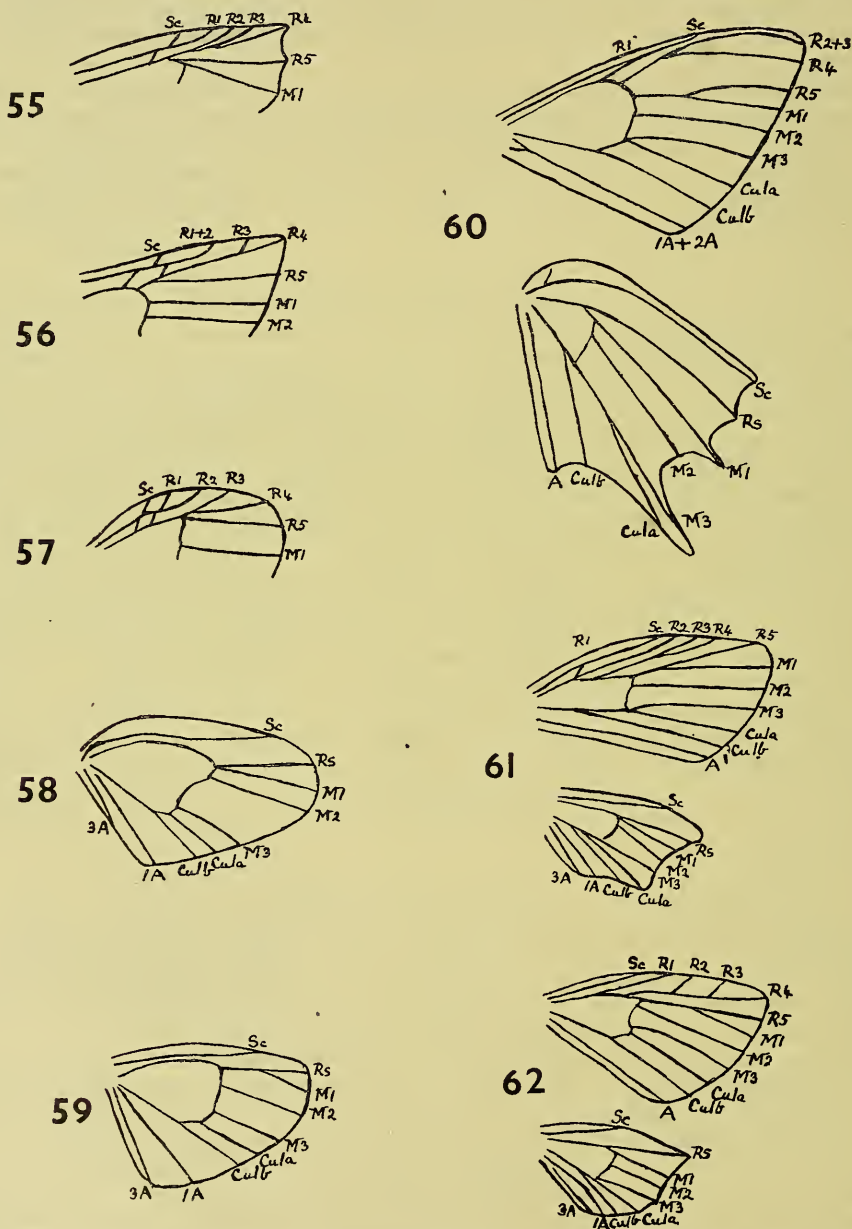


Fig. 55.—*Boarmia lyciaria* Gn. Fig. 56.—*Crypsiphona occultaria* Don. Fig. 57.—*Eumelia rosalia* Stoll. Fig. 58.—*Monoctenia falernaria* Gn. Fig. 59.—*Diceratucha xenopis* Low. Fig. 60.—*Nyctalemon patroclus* Lin. Fig. 61.—*Lobogethes interrupta* Warr. Fig. 62.—*Epiplema instabilata* Wlk.

Two subfamilies may be recognized, the Arctiinae and Lithosiinae, the former with the thorax and abdomen stout and usually hairy, the latter with these slender and usually smooth. These are differences of apparently little morphological value, but they represent two distinct lines of evolution, and the division is a natural one.

The Noctuidae is an immensely numerous family, but one which presents comparatively small structural variations, the neuration being almost uniform in the great majority of its genera. In the forewing R1 arises from the cell and does not anastomose; the areole is present in probably nine-tenths of the genera, and R2 generally arises from it separately, but the areole may be lost either by coalescence or dissociation. In the hindwing the subcostal and radius arise separately from the base of the wing, but anastomose very soon, usually at a point only, but in some cases the anastomosis is prolonged as far as the middle of the cell (Figs. 68-70).

The internal classification of the family is difficult. It is divisible into two groups, Trifidae and Quadrifidae (Caradrinidae and Plusiidae of Meyrick), but these are not sharply defined. In the former, M2 of the hindwing has retained its median position, but has become vestigial. In the latter, M2 has been displaced towards, or as far as, the lower angle of the cell and remains fairly or strongly developed. There are, however, intermediate genera. The classification by Hampson into eleven subfamilies is convenient and for the most part natural, but they are not sharply defined and, therefore, incapable of strict definition. The Agaristidae have been considered a distinct family, but without justification. They are merely day-flying noctuids, and are not separated by any sharp

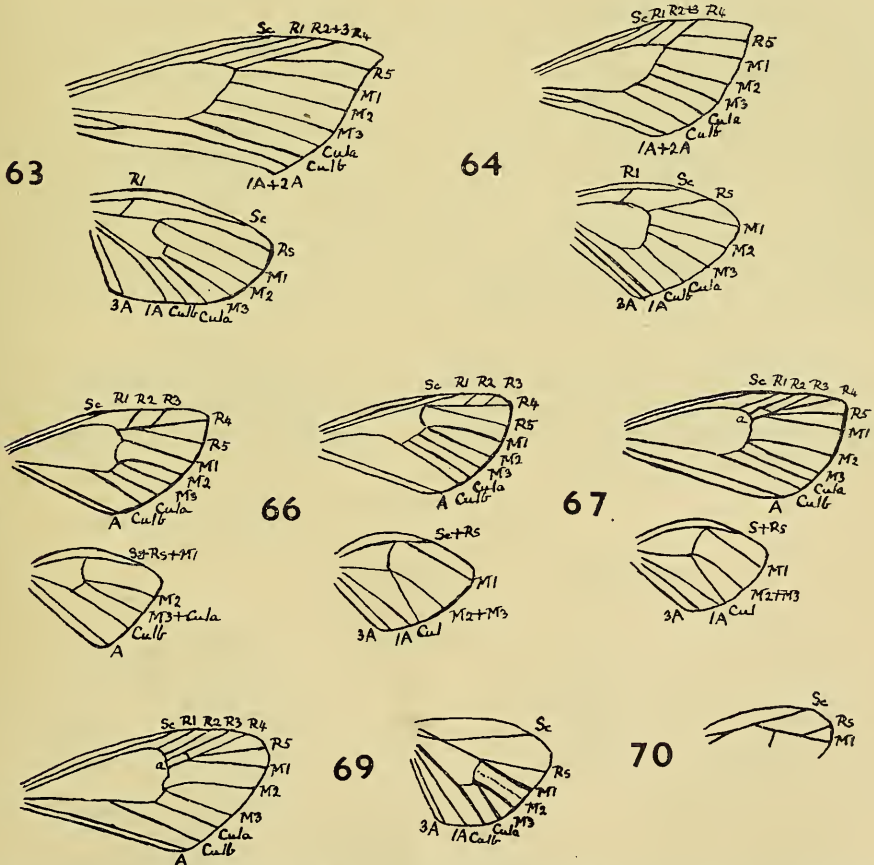


Fig. 63.—*Herse convolvuli* Lin. Fig. 64.—*Hopliocnema brachycera* Low. Fig. 65.—*Syntomis annulata* Fab. Fig. 66.—*Euchromia creusa* Lin. Fig. 67.—*Utetheisa pulchella* Lin. Fig. 68.—*Mocis frugalis* Fab. Fig. 69.—*Cosmodes elegans* Don. Fig. 70.—*Earias parallela* Luc.

line from the rest of the family. The Noctuidae cannot have been derived from any existing family, but probably arose from low down on the hypsid stem. The most primitive subfamily is perhaps the Hyblaeinae, which has well-developed maxillary palpi (alone in the Noctuoidea), but has lost the areole. The apparently rather close affinity of the Noctuidae with the Arctiadae is probably partly due to convergence.

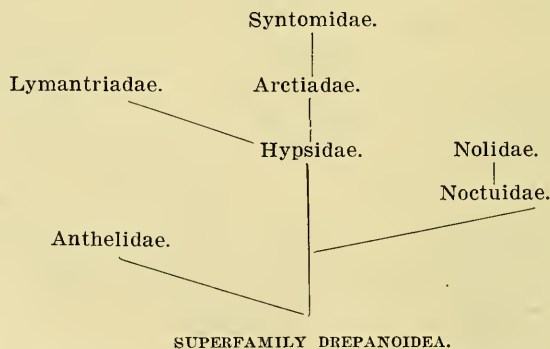
Convergence is still more noticeable in the Nolidae, a small family which cannot be distinguished from the Arctiadae by neurulation. There is no areole in the forewing; in the hindwing the subcostal and radius are completely fused from the base to about the middle of the cell; in other respects there is not much variation in the neurulation. A minor but constant characteristic is the presence of tufts of raised scales on the forewings. They appear to be directly derived from the Noctuidae, perhaps from the Sarrhrothripinae.

Another small family is the Hypsidae, which is important as the direct ancestor of the Arctiadae. It differs from that family in the subcostal of the hindwing being separate from the radius from the base, but connected with it at about one-fourth by R1 or by an anastomosis (Fig. 71).

The Lymantriadae is a family of some size distinguished from the Hypsidae by the absence of the tongue, and following a different line of development. Many of the genera have retained the areole, but many have lost it, usually by coalescence, but in a few by dissociation. In the hindwing the subcostal is approximated to the radius and connected with it by R1 (Fig. 72).

The Anthelidae (Turner, 1921) is an Australian family of sixty or seventy species. In this family the tongue is absent in all but one genus. The frenulum is present in the male but absent in the female. In the forewing an areole is always present; in form it is rather large and elongate so as to reach nearly to the apex of the wing (Figs. 73, 74). At the base of the hindwing the subcostal is widely separated from the radius and usually remains so, but may be less widely separate opposite the middle of the cell. Normally these veins are connected by R1, but this may be weakly developed or absent. The most characteristic feature in the neurulation is a cross-bar from R2 to R3 at the distal end of the areole, a new development peculiar to this family (Fig. 73). In the two following genera this cross-bar extends from R1 to R3; *Gephyroneura* (Fig. 75), in which the proximal half of the areole has coalesced leaving a triangular distal portion fully developed; and *Munichryia* (Fig. 74), which is the only genus possessing a well-developed tongue.

The Anthelidae is a specialized group, which has retained some archaic peculiarities. It cannot have been derived from, or given rise to, any existing family, but probably is an early branch from the stem which gave rise to the Hypsidae and Lymantriadae. The following scheme illustrates my conception of the relationships of the families of the Noctuoidea.



There is no median vein in the cell and Cu2 is absent in both wings. Forewings with M2 from lower angle of cell. Hindwings with subcostal closely approximated to Rs near its origin. 3A short or absent.

There are two families. The Callidulidae is a small family of day-flying moths represented in India (Hampson, 1892). In them the antennae are simple and the palpi long and slender. The frenulum is sometimes short or absent. In the hindwings the cell is open; 3A is present, M2 and M3 are stalked, Rs and M1 are stalked, the subcostal is bent so as nearly to touch Rs near this point; and there may be a minute precostal spur (Fig. 78). The areole, though generally lost, is present in one genus.

The Drepanidae is a family of no great size, which presents considerable structural variation. The palpi are slender and often minute. Tongue, frenulum and areole may be present or absent. In the hindwing Rs arises well before angle of cell approximated to or (in *Amphitorna*, Fig. 81) anastomosing with the subcostal, the cell is closed and 3A may be absent; when present, it is short and usually runs to dorsum. In *Oreta* (Fig. 80) the areole is very long, reaching nearly to apex of forewing, and extremely narrow.

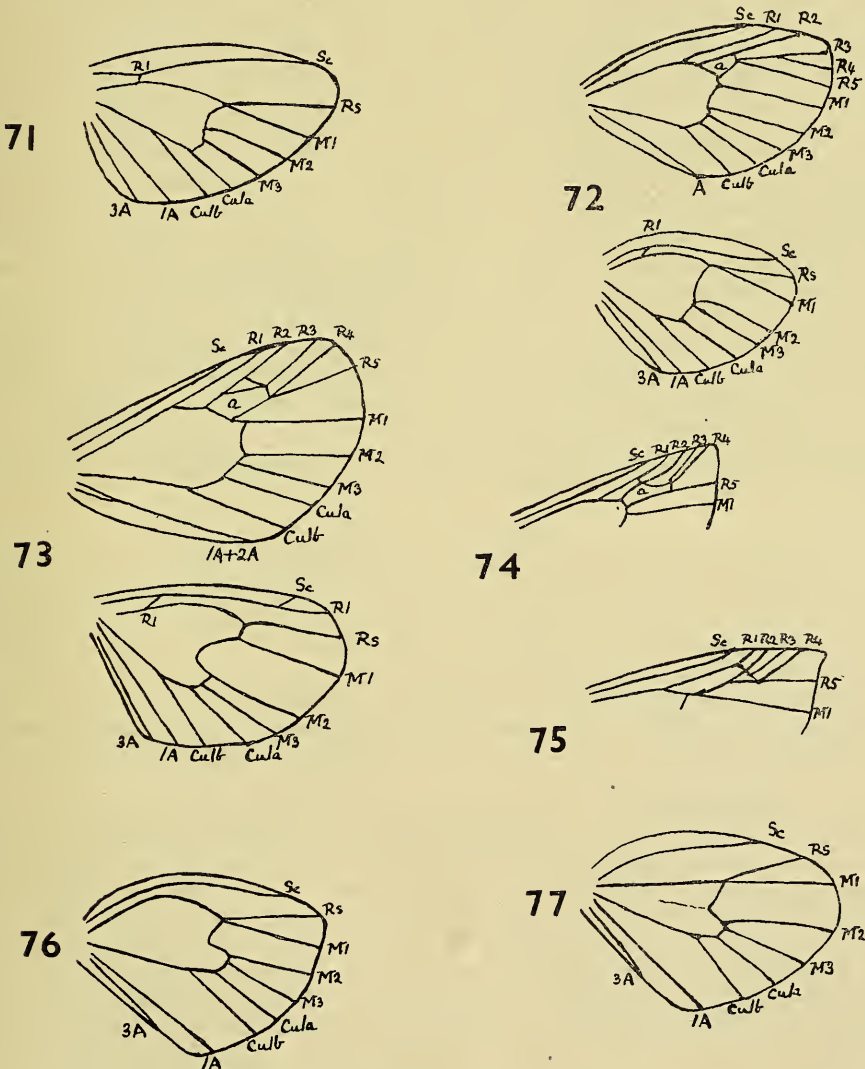


Fig. 71.—*Hypsa alciphron* Cram. Fig. 72.—*Laelia obsoleta* Fab. Fig. 73.—*Anthela ferruginosa* Wlk. Fig. 74.—*Munichryta senicula* Wlk. Fig. 75.—*Gephyroneura cosmia* Turn. Fig. 76.—*Pterolocera amplicornis* Wlk. Fig. 77.—*Nataxa flavifascia* Wlk.

This superfamily is of comparatively small extent and more nearly allied to the Noctuoidea than to any other, but should not be included with this superfamily. The neurational resemblances to the Pyraloidea are an example of convergence, the two groups being genetically widely separate. The suggestion that the Callidulidae is in any way nearly related to the Rhopalocera is in my opinion equally unfounded.

SUPERFAMILY LASIOCAMPOIDEA.

Of these I recognize only one family, the Lasiocampidae, which is found in all continental areas. The family is sharply distinguished from the Bombycoidea by the approximation of the origins of M2 and M3, though it has specialized, like some families of that group, by the loss of the frenulum. The areole has been lost by coalescence, not by dissociation, as I at one time supposed (1918), for that would have left R2 stalked with R3 and R4 with R5, but, on the contrary, while R2 and R3 are stalked as in other Sthenochorda, R4 remains a separate vein in nearly all the genera (Figs. 82, 83). The exceptions are the Indian genus *Bhima* and the European genus *Endromis* (Fig. 84), in which as a secondary change R4 has become stalked with R2 and R3, and the Australian *Aprosepta* Turn., in which it is stalked with R5. The basal expansion of the costal base of the hindwing, which compensates for the absence of the frenulum, is often large and usually contains one or more, and occasionally many, basal costal pseudoneuria, evidently for the purpose of strengthening this part of the wing. These are very irregular in form as well as in number, being frequently branched, and cannot therefore be due to the persistence of the humeral veinlet present in the Homoneura (Figs. 85, 86). On the contrary, the presence of these substitutes indicates that this veinlet has been irrevocably lost. In most of the genera there is a strong anastomosis enclosing a basal accessory cell between the subcostal and radial sector of the hindwing. As in other groups, this anastomosis has replaced the vein R1, which is still present in a few genera. The most primitive in this respect is *Endromis* (Fig. 84), in which a short R1 is present as occurs in many other families. For the strengthening of this part of the wing two lines of evolution have developed: (1) a strong anastomosis with a moderate accessory cell in most genera, or (2) a grossly exaggerated accessory cell with retention of R1 as in *Perna* (Fig. 83).

I see no sufficient justification for retaining the Endromidae as a separate family containing the single genus *Endromis*.

SUPERFAMILY PSYCHOIDEA.

Tongue absent. Frenulum developed. In both wings a median vein, which may be either single or forked, is present in the cell. In the forewings M1 arises from the middle of the cell or slightly above, M2 is approximated to, or connate with, M3, and R3 and R4 are stalked or rarely coincident. In the hindwings M2 is connate, stalked, or coincident with M3. Cu2 is present in both wings.

In this and the two following superfamilies the median vein persists in the cell, but chorda and areole are never present in the Psychoidea. It consists of two families, one specialized, the other more generalized, both probably ancient offshoots of a common stock.

In the Psychidae the female never leaves the larval case, and has usually degenerated into little more than an egg-sac, though antennae and legs are present in the most primitive genera. In both sexes the tongue and palpi are absent. The neururation of the male is in most cases highly peculiar, but this is not so in the most primitive genera. Of these *Aprata* (Fig. 87) from Ceylon is a good example. Here the neururation is of a generalized character. The European genus *Fumea* (Fig. 88) differs in the loss of the lower branch of the median in the cell of both wings, the coincidence of R3 and R4 of the forewings, and the loss of one of the branches of the median beyond the cell in the hindwings. In the great majority of genera the forking of the median is preserved in the cell of both wings. Their neururation in some respects shows features unique in the Lepidoptera. In most, the combined first and second anals of the forewing run upwards to fuse with the second cubital. The second anal may be continued beyond its anastomosis even to the wing margin, and sometimes several veinlets or pseudo-

neuria arise running from the combined anal vein towards the dorsal margin. In *Clania ignobilis* (Fig. 90) the combined R1 and subcostal anastomose with Rs near the wing margin, a remarkable character. These developments appear to have arisen to strengthen the areas of wing affected. They are probably adaptational and therefore only of minor genetic significance. Accessory veinlets, variable in number, may develop, running towards the dorsum of the forewing and the costa of the hindwing.

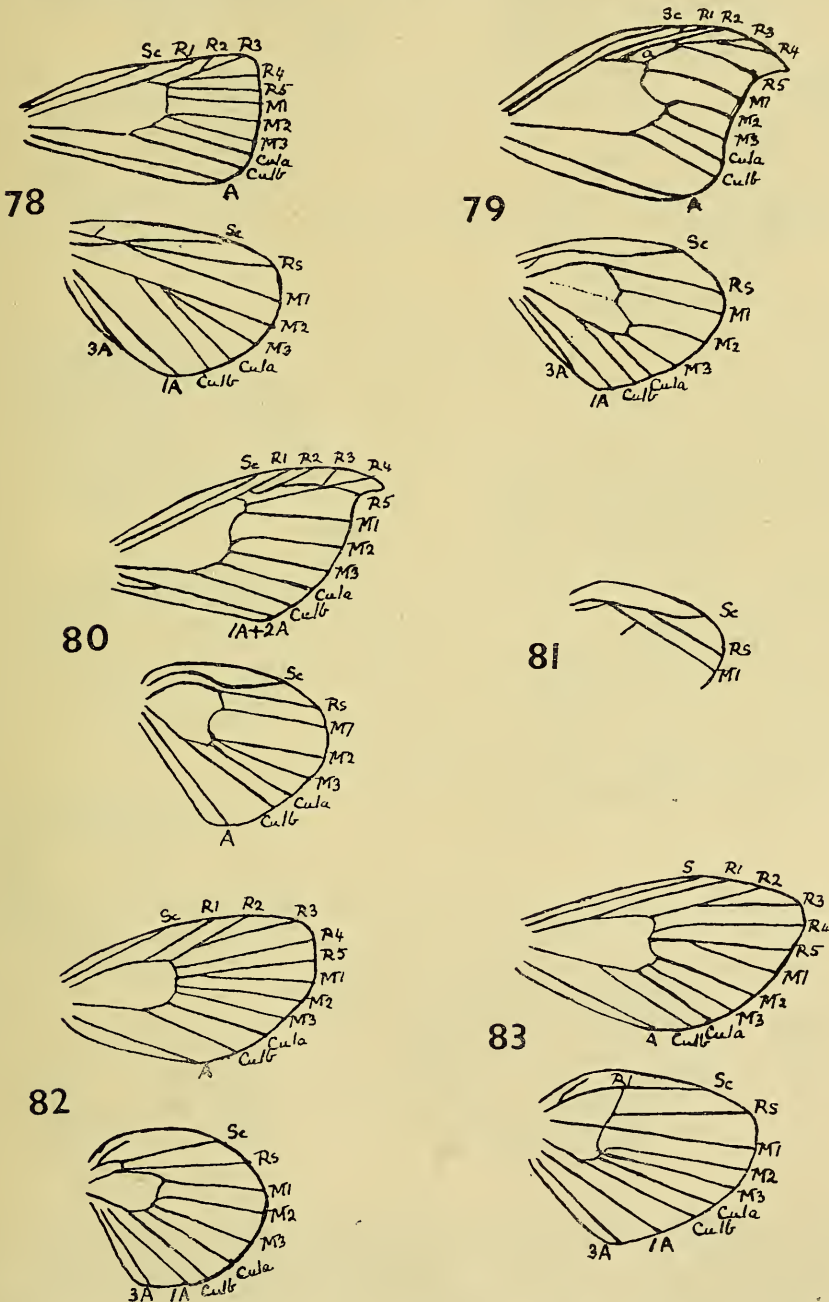


Fig. 78.—*Callidula erycinoides* Wlk. (after Hampson). Fig. 79.—*Falcaria falcataria* Lin. (after Meyrick). Fig. 80.—*Oreta jaspidea* Warr. Fig. 81.—*Amphitorna lechriodes* Turn. Fig. 82.—*Eriogaster rubi* Lin. (after Meyrick). Fig. 83.—*Perna exposita* Lewin.

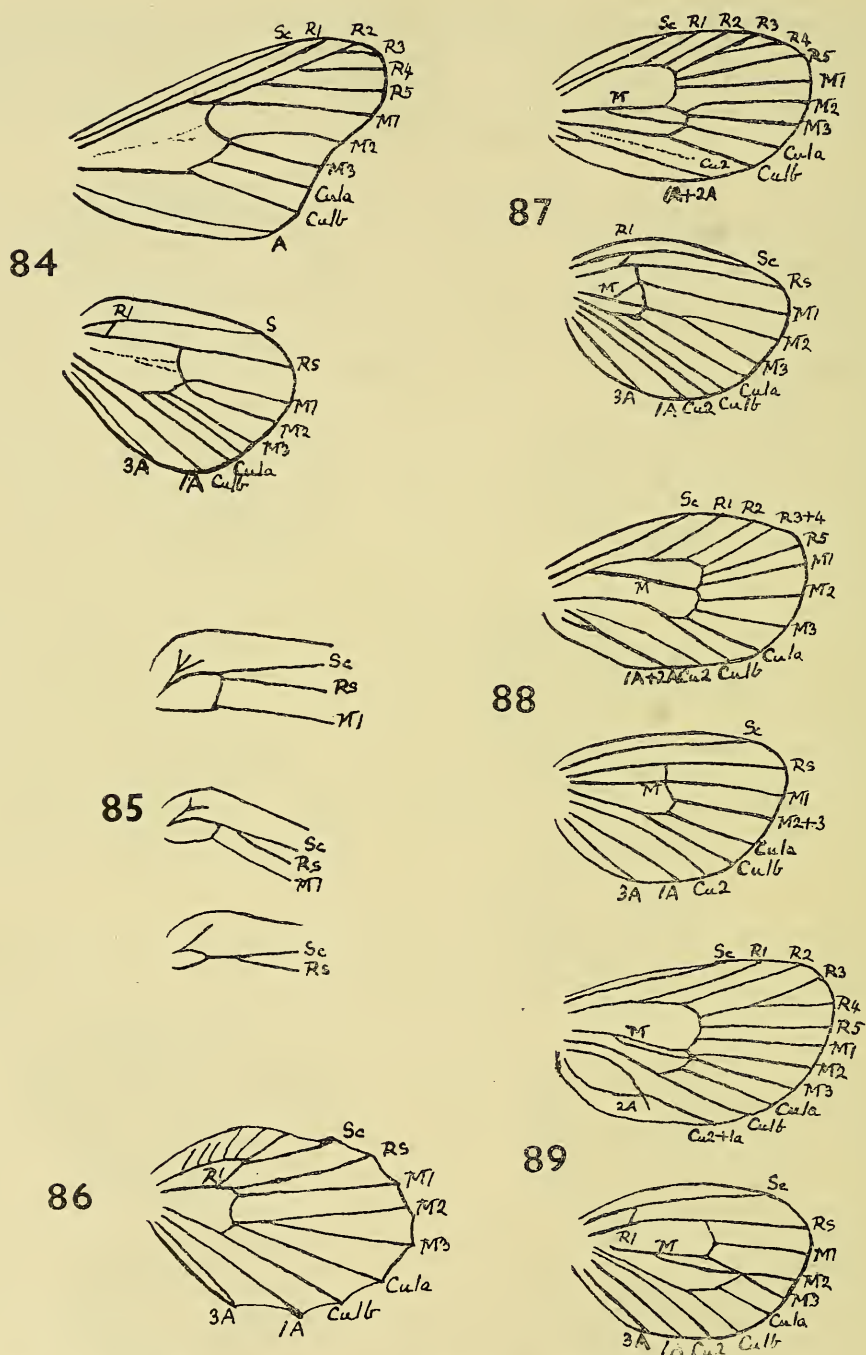


Fig. 84.—*Endromis versicolora* Lin. (after Meyrick). Fig. 85.—Humeral angle of hindwing in three genera of Lasiocampidae. a. *Porola arida* Wlk. b. *Crexa subnotata* Wlk. c. *Bombycomorpha pallida* Dist. Fig. 86.—*Gastropacha quercifolia* Lin. (after Meyrick). Fig. 87.—*Aprata mackwoodi* Moore (after Hampson). Fig. 88.—*Fumea casta* Pall. (after Meyrick). Fig. 89.—*Plutorectis lurida* Heyl.

In the Limacodidae the median vein in the cell of the forewings is usually, but not always, single; in the hindwings it is always unbranched. There is not much variation in the neuration, the most important being in R1 of the hindwings, which is present in the older genera, but in many is replaced by an anastomosis (Figs. 91, 92). Although the frenulum is well developed, the base of the hindwings may be rather strongly curved and in some cases fine pseudoneuria from the subcostal have developed, analogous to those in the Lasiocampidae.

SUPERFAMILY CASTNIOIDEA.

In this group the labial palpi are well developed. The tongue may be present or absent. The antennae are smooth and dilated or clubbed at their apices. A forked or single median vein is present in both wings. In the forewing Cu2 is present and M2 is approximated at its origin to M3.

Of the two families of which it is composed the Castniidae is the more primitive. In this family the cell is closed in both wings; Cu2 and two anal veins are present in the hindwings; and there is a well-developed areole in the forewings (Figs. 94, 95). The family is exclusively neotropical.

The family Tascinidae has lost the areole, and the cell is open in the hindwings, and sometimes in the forewings also. The hindwings have two anal veins, but Cu2 is absent. The family is represented in Australia by the genus *Synemon* (Fig. 93) and in Malaya by two closely allied genera, *Tascina* (Fig. 96) and *Neocastnia*. In the latter two the hindwing neuration shows complete absence of the discocellulars so that the median vein and its lower branch (the upper branch being obsolete), with its sub-branches M2 and M3, are isolated. The cell of the forewings is open in its costal half. In *Synemon* the cell is closed in the forewings; in the hindwings the discocellular between M1 and M2 is absent, but the connection between M3 and Cu1a is retained.

Members of the superfamily Castnioidea are day-flying moths often on the wing in bright sunshine, and with this appears to be correlated their clubbed antennae and superficial form, which have suggested some affinity with the Hesperidae and other Rhopalocera. An examination of the neuration is sufficient to dispel this supposition. In reality there are hardly two groups of the Lepidoptera more distinct. The superfamily is isolated, and probably an ancient development from the same stem as the Cossioidea, which are their nearest allies. This is strongly confirmed by the little we know of their larvae. That of a species of *Castnia* is an internal feeder in the stem of one of the Bromeliaceae (Westwood, 1877); that of a *Synemon* forms tunnels among the roots of grasses and sedges (Tindale, 1928). Both pupate in cocoons, those of the latter being underground.

SUPERFAMILY COSSOIDEA.

Tongue absent. Labial palpi moderate, short, or absent. Frenulum usually present. Forewings with areole usually well developed, but sometimes small or absent, a strong median vein in cell usually forked, M2 from nearer M3 than M1, Cu2 usually present, and A1 coalescing with A2 near base. Hindwings with median vein in cell usually forked, R1 joining Sc at or near end of cell, but sometimes absent, Cu2 present, two or three anal veins, A1 and A2 coalescing near base or wholly fused. The larvae are wood-borers.

The genera *Cossodes* and *Dudgeona*, with their primitive neuration and well-developed palpi and tibial spurs, are not far from the point at which the Sthenochorda and the Asthenochorda diverged by the loss of the primitive five-jointed maxillary palpi in the former.

I have dealt fully elsewhere with the Cossidae (1918), so that it is necessary to deal here only with two small allied groups. Two genera from Madagascar have lost Cu2 in both wings, and have been separated by Hampson as the Argyrotypidae. In other respects they agree with the Cossidae, and should, I think, be included in that family. The Arbelidae are represented by some thirty or more species in Africa and India. They have lost the frenulum. The median is unbranched in both wings, there is no areole, and Cu2 is absent in both wings. The larvae are wood-borers.

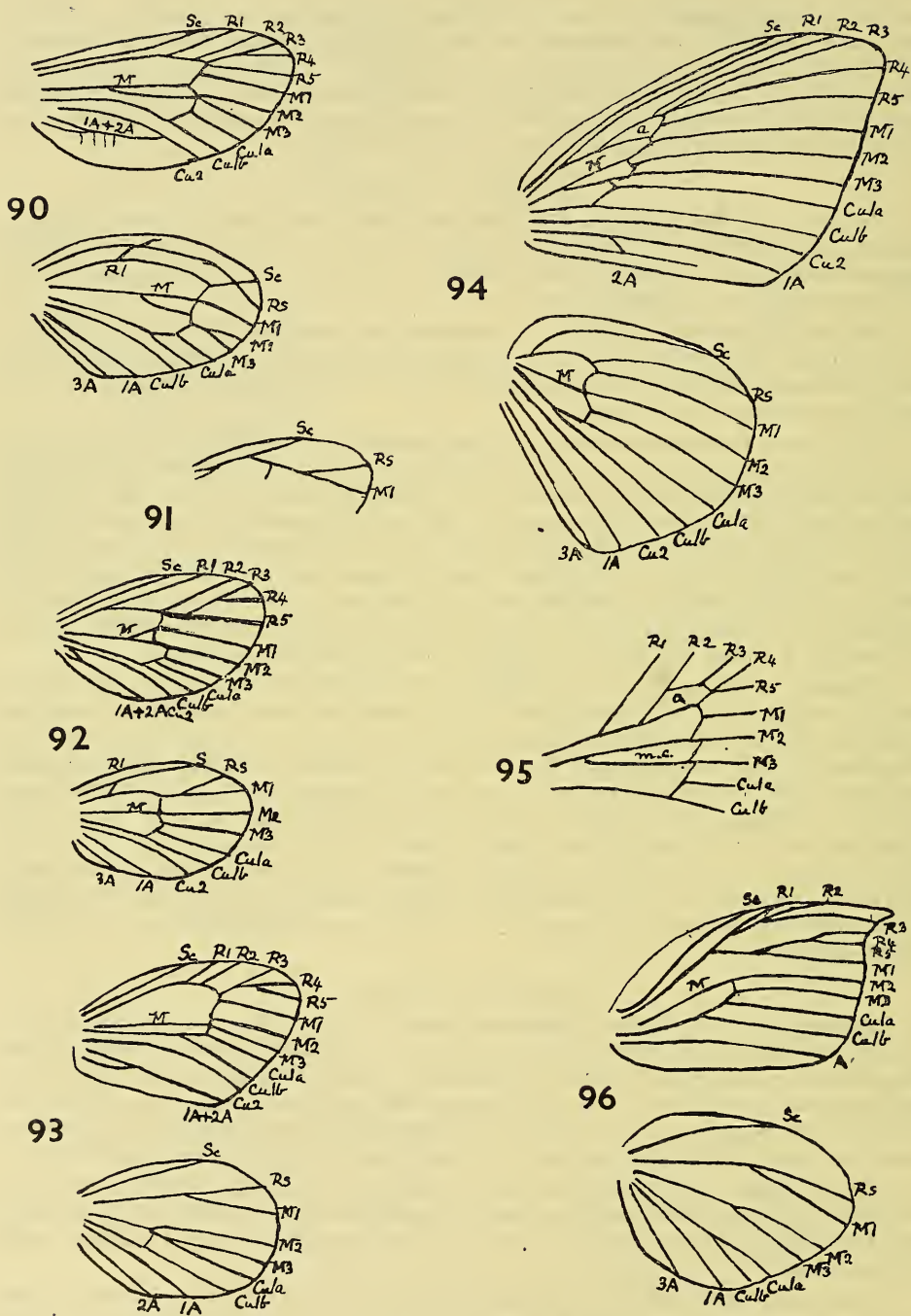


Fig. 90.—*Clania ignobilis* Wlk. Fig. 91.—*Doratifera vulnerans* Lewin. Fig. 92.—*Susica humeralis* Wlk. Fig. 93.—*Synemon collecta* Swin. Fig. 94.—*Castnia cacica* H-Sch. (after Westwood). Fig. 95.—*Gazera linus* Fab. Forewing. Fig. 96.—*Tascina orientalis* West.

CONCLUSION.

This concludes my review of the classification of the Lepidoptera. It has, I know, some weak points, but I am confident that it represents an advance in the classification of this Order of insects. Few, perhaps, will accept its conclusions on a first reading, but it will deserve attention by anyone who attempts a future classification. I cannot conclude without expressing the debt I owe to Dr. R. J. Tillyard, whose brilliant researches inspired me to make this attempt, which I have long meditated. I grieve that he is no longer among us to read it and send me his criticisms.

A SUMMARY OF THE CLASSIFICATION PROPOSED.

This does not contain all the families of the Lepidoptera, for I have thought it wiser to omit some, of which I have insufficient knowledge, but contains those known to occur in Europe, Australia and New Zealand, with a few that are known only from other regions.

Suborder HOMONEURA.

- Superfam. Micropterygoidea.
 - Fam. Micropterygidae.
 - Eriocranidae.
 - Mnaesarchaeidae.

- Superfam. Hepialidoidea.
 - Fam. Prototheoridae.
 - Anomosetidae.
 - Palaeosetidae.
 - Hepialidae.

Suborder HETERONEURA.

Division ASTHENOCHORDA.

Subdivision *Rhopalocera*.

- Superfam. Hesperoidea.
 - Fam. Hesperidae.
- Superfam. Papilionoidea.
 - Fam. Papilionidae.
- Superfam. Nymphaloidea.
 - Fam. Nymphalidae.
 - Pieridae.
 - Lycaenidae.

Subdivision *Microptila*.

- Fam. Elachistidae.
 - Subfam. Coleophorinae.
 - Scythrinae.
 - Elachistinae.
 - Douglasianae.
 - Cosmopteryginae.
- Fam. Gelechiidae.
 - Subfam. Hyponomeutinae.
 - Amphitherinae.
 - Thalmarcellinae.
 - Oecophorinae.
 - Blastobasinae.
 - Gelechianae.
 - Xyloryctinae.
- Fam. Tortricidae.
 - Subfam. Chlidanotinae.
 - Eucosminae.
 - Tortricinae.
 - Phalonianae.

Suborder HETERONEURA.

Division ASTHENOCHORDA.

Subdivision *Microptila*.

(Continued.)

- Fam. Copromorphidae.
 - Subfam. Copromorphinae.
 - Carposininae.
- Fam. Aegeriidae.
- Fam. Glyphipterygidae.
 - Subfam. Glyphipteryginae.
 - Heliodininae.
 - Heliozelinae.
- Fam. Plutellidae.
 - Subfam. Plutellinae.
 - Epermenianae.
 - Gracilariinae.
- Fam. Tineidae.
 - Subfam. Adelinae.
 - Lamproninae.
 - Tineinae.
 - Lyonetianae.
 - Oposteginae.
 - Cyclotorninae.
 - Epipyropinae.
- Fam. Nepticulidae.
- Superfam. Pterophoroidea.
 - Fam. Orneodidae.
 - Pterophoridae.
- Superfam. Pyraloidea.
 - Fam. Thyrididae.
 - Phycitidae.
 - Galleriidae.
 - Crambidae.
 - Schoenobiadae.
 - Pyralidae.
 - Pyraustidae.
 - Tineodidae.
- Superfam. Zygaenoidea.
 - Fam. Zygaenidae.

Division STENOCHORDA.	Superfam. Drepanoidea.
Superfam. Cossioidea.	Fam. Callidulidae.
Fam. Arbelidae.	Drepanidae.
Cossidae.	Superfam. Sphingoidea.
Superfam. Castnioidea.	Fam. Sphingidae.
Fam. Castniidae.	Superfam. Uranoidea.
Tascinidae.	Fam. Uranidae.
Superfam. Psychoidea.	Epiplemidae.
Fam. Psychidae.	Superfam. Geometroidea.
Limacodidae.	Fam. Oenochromidae.
Superfam. Lasiocampoidea.	Boarmiadae.
Fam. Lasiocampidae.	Geometridae.
Superfam. Noctuoidea.	Sterrhidae.
Fam. Anthelidae.	Larentiidae.
Noctuidae.	Superfam. Bombycoidea.
Nolidae.	Fam. Saturniidae.
Hypsiidae.	Bombycidae.
Lymantriidae.	Brahmaeidae.
Arctiidae.	Cymatophoridae.
Syntomidae.	Notodontidae.

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